PATTERNS OF VEGETATION CHANGE IN SOUTHWEST VICTORIA (AUSTRALIA) OVER THE LAST TWO GLACIAL/INTERGLACIAL CYCLES: EVIDENCE FROM LAKE WANGOOM

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HARLE, K.J., KERSHAW, A.P. & CLAYTON, E., 2004:11:14. Patterns of vegetation change in southwest Victoria (Australia) over the last two glacial/interglacial cycles: evidence from Lake Wangoom. *Proceedings of the Royal Society of Victoria* 116(1)105-137. ISSN 0035-9211.

Multivariate statistical techniques and modern analogue analysis of the Lake Wangoom pollen record were used to reconstruct vegetation change in western Victoria (Australia) over the last 200,000 years. Stratigraphically unconstrained correlation coefficient analysis was used to compare the representation of pollen taxa throughout the sequence. Ten *pollen associations* have been determined, from which it is possible to identify vegetation community types represented in the record. These include elements of warm temperate rainforest not previously suspected as having occurred in the region during the Late Quaternary. A stratigraphically unconstrained dissimilarity coefficient analysis was used to compare pollen spectra in the sequence. From this, thirteen key *pollen assemblages* have been identified. Inverse analysis of pollen taxa was undertaken to produce *pollen associations* representing the mosaic of vegetation types present in the region at the time of sediment deposition. Interpretation of the *pollen assemblages* was assisted using modern analogue analysis.

The record reveals a complex pattern of cyclical shifts in the composition of the vegetation in the region overlain by long term trends in vegetation composition. Three major and distinct phases of forest and woodland expansion, which chronologically equate to the Holocene, Last Interglacial and latter part of the Penultimate Interglacial, have been identified. In addition, an apparently short phase of *Eucalyptus* and rainforest expansion occurred during the Penultimate Glacial period. This is distinguished from the other forest phases by its high representation of a distinctive type of Asteraceae, which is commonly associated with glacial complexes. Open grassland, heath and herbfield communities were widespread during the driest glacial phases, with limited occurrences of semi-arid woodland and scrub. Dry sclerophyll forest, woodland and temperate grassland communities expanded during climatically intermediate phases. A trend to more open-canopied vegetation in the last ca 50 kyrs may be related to increased levels of burning, possibly anthropogenic and/or volcanic in origin.

Key words: Quaternary, vegetation, pollen, southwest Victoria, multivariate statistical analysis, modern analogue

THE PRESENT native vegetation of the Western Victorian volcanic plains is characterised by sweeping grasslands, scattered stands of eucalypt-dominated woodland and dry sclerophyll forest and remnant patches of Casuarinaceae woodland. Palynological records from the region indicate that this has not always been the case, with evidence for short term as well as long term shifts in the composition and relative importance of various vegetation types (see Kershaw et al. this volume). Even within the recent past there is clear evidence in these records that co-lonial settlers had a drastic effect on the regional vegetation. Sharp decreases in arboreal taxa associated with increases in Poaceae provide evidence for tree clearance and establishment of open pasture, whilst the appearance of exotic species, such as *Pinus*, attest to the establishment and spread of introduced species (D'Costa et al. 1989; Dodson, 1974a; Edney et al. 1990; Gell et al. 1994; Kershaw et al. this volume). Going further back in time, Holocene sequences indicate that open *Eucalyptus* woodland was dominant in western Victoria during the middle to
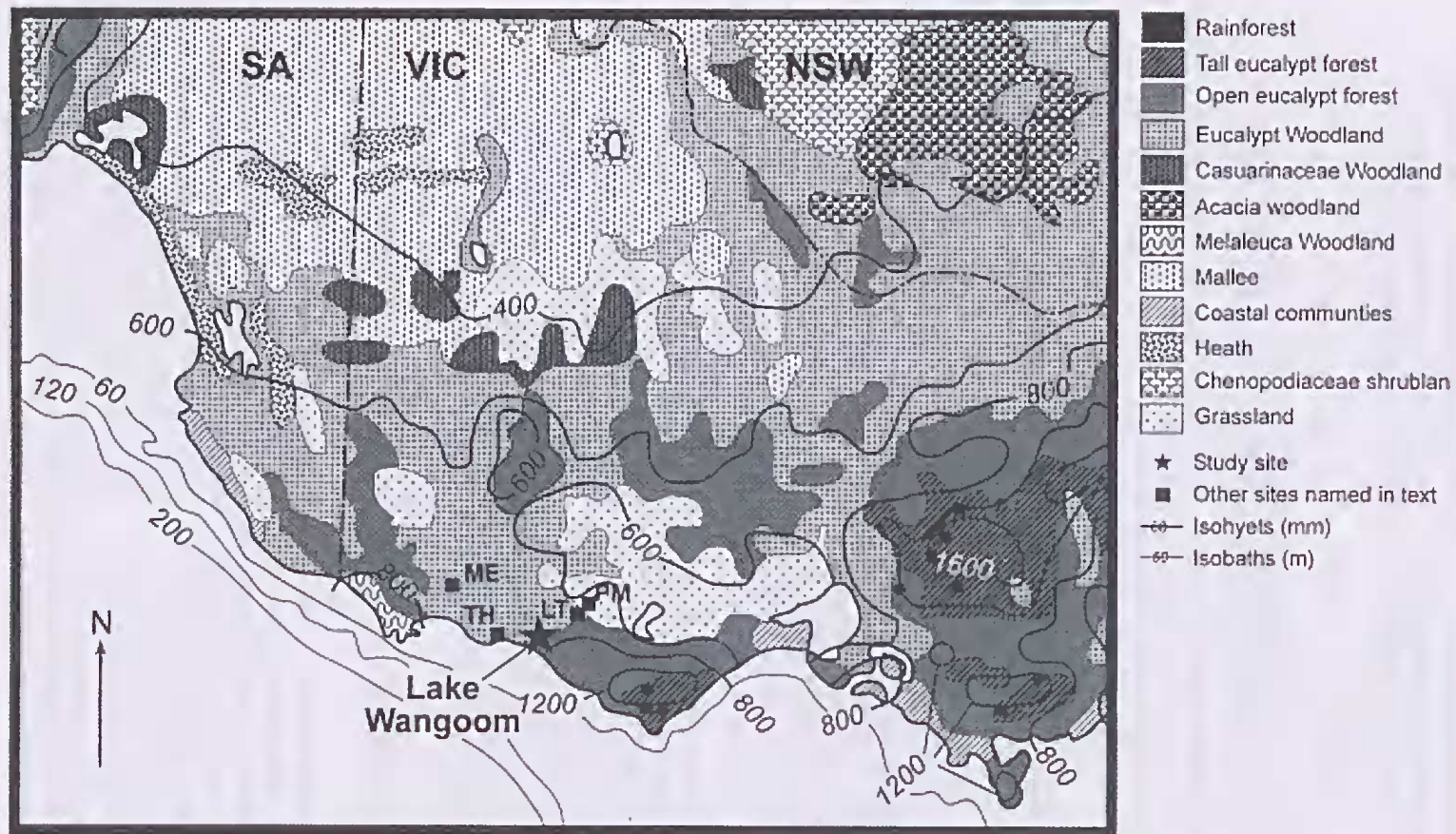
Fig. 1. Map of the study region showing pre-European regional vegetation (after the Australian Surveying and Land Information Group, 1990), mean annual precipitation (mm/yr) (Parkinson, 1986), the study site and other sites mentioned in the text. (ME) Mount Eccles, (TH) Tower Hill, (LT) Lake Terang, (PM) Pejark Marsh.

late Holocene, whilst Casuarinaceae dominated communities were more widespread during the early Holocene (eg. Crowley & Kershaw 1994; D'Costa, et al. 1989; Dodson 1974a; Edney et al. 1990; Head 1988; Luly 1993). In contrast, trees were sparse during the height of the Last Glacial period, with open semi-arid steppe, herbfield and scrub communities dominant (D'Costa et al. 1989; Crowley & Kershaw 1994; Dodson 1979; Edney et al. 1990; Harle et al. 1999). Unfortunately, there are very few pre-Holocene records from the region. Of these, the Lake Wangoom sequence provides the longest and most continuous late Quaternary record, extending from the Penultimate Interglacial to the present (Harle et al. 2002; Harle 1998). Other records from the region of similar or longer duration are either very discontinuous (Lake Terang, D'Costa & Kershaw 1995) or do not extend into the Late Pleistocene (Pejark Marsh, Wagstaff et al. 2001; Kershaw et al. this volume). The Lake Wangoom record, therefore, is extremely important to the reconstruction of late Quaternary environments in western Victoria.

Previous interpretation of the Lake Wangoom record has been largely based on the representation of a limited number of significant taxa, with the focus on broad-scale vegetation changes in response to climate fluctuations as well as on questions of chronology (Edney et al. 1990; Harle et al. 1999; Harle et al. 2002). This paper presents a much more detailed analysis of a 41 m long pollen record from the site, utilising the full range of dryland palynomorphs identified. The interpretation of this large dataset is complicated by uncertainty over the relationships between pollen spectra and source vegetation as well as the difficulty in recognising many Australian palynomorphs beyond generic or even family level. These uncertainties have implications for the reconstruction of vegetation communities. The problem is exacerbated in long records, such as the Lake Wangoom sequence, where questions over species and community extinction become apparent with influences such as long-term climate change and anthropogenic activities, including use of fire.

Two approaches have been adopted in this study in an attempt to overcome some of the difficulties associated with interpreting such a complex dataset. Firstly, multivariate statistical analyses have been applied to the Lake Wangoom palynostratigraphy, based on the assumption that pollen taxa with frequent co-occurrence in fossil assemblages are more likely to have been associated in life than those that are not (Harris and Norris 1972). From this analysis,

pollen associations and assemblages were identified, the former being used to provide evidence of source vegetation communities (including those now locally extinct) and the latter to determine the mosaic of communities making up the regional vegetation. To enhance these findings, a second approach was also adopted using modern analogue analysis. This entailed the quantitative identification of closest modern analogues for each fossil pollen assemblage using the Southeast Australian Recent Pollen Database developed by Kershaw et al.(1994a) and D'Costa & Kershaw (1997). The combined results are used to provide a detailed reconstruction of dryland regional vegetation in western Victoria over the last 200,000 years.

SITE LOCATION AND REGIONAL VEGETATION

Lake Wangoom (142°36' E 38°21'S, altitude 100 m asl) is located on the southern margin of the western Victorian volcanic plains, 9.5 km from the coast (Fig. 1). It is a simple volcanic maar approximately 1200 m in diameter (Ollier 1967) which has been partially filled by sediment (Edney et al. 1990). Prior to European settlement in the 1840s, Lake Wangoom had a water depth of around 8 m (Bonwick 1970). It is currently drained and is dry in all but the wettest winters.

Regionally, Lake Wangoom is located within a broad climatic and vegetation gradient trending southeast to northwest (Fig. 1). Variation in the vegetation is influenced by climate, soils and human impact. Drier communities generally occur in the western and north-central areas. Wet forest communities, largely dominated by *Eucalyptus*, are widespread in the east and southeast. Temperate rainforest, dominated by *Nothofagus cunninghamii*, grows in isolated patches in the Otway Ranges and the Central Highlands. Since European settlement in the 1840s (Sayers 1972), the natural vegetation of western Victoria has been extensively cleared, mainly for pasture, and exotic species (eg. *Pinus radiata* and *Cupressus* spp.) have been introduced.

METHODOLOGY

Core collection and sampling
The Lake Wangoom pollen record has been constructed from a combination of cores extracted from

the centre of the site. The majority of the sequence described is based on a 41.5 m long core (LW87) collected in 1987 using a Speedstar percussion drilling rig. Unfortunately, the top 1.8 m and sediments between 8.5 and 11 m were not recovered. These gaps were filled using samples from a 20.6 m core (LW84) originally analysed by Edney (1987), and collected in 1984 using a Gemco drilling rig and a Livingstone sampler.

The LW87 core was sampled for sediment, pollen and charcoal analyses at 20 cm intervals. The top 1.8 m of the LW84 core was sampled at 10 cm intervals and sediments between 8.5 and 11 m at 20 cm intervals.

Dating

A chronology for the record has been established using radiocarbon and uranium/thorium disequilibrium techniques. Sampling, methods and results of the application of dating to this record are described and discussed in Harle et al. (2002). Dates acquired are shown in Fig. 4.

Sediment analyses

The sediments of the Lake Wangoom 41.5 m core were analysed for organic, inorganic and carbonate contents through combustion of oven dried samples in a muffle furnace at 550 °C and 1000 °C respectively, with the residue after ignition representing the inorganic and carbonate content.

The magnetic susceptibility of the sediments was measured using the Bartington Magnetic Susceptibility Meter (Bartington 1983). Susceptibility readings were corrected for magnetic drift, diamagnetism and sample mass. Results are plotted in Fig. 4.

Pollen and charcoal analyses

Samples (1 cm^3) were prepared for pollen and charcoal analyses using the standard methods of potassium hydroxide digestion, hydrofluoric acid treatment and acetolysis (Faegri & Iverson 1989). The palynological residues were mounted on microscope slides in silicon oil (AK2000) and counted on a BH Olympus microscope at x600 magnification until a minimum of 150 pollen grains and spores of taxa included in the pollen sum was achieved. Based on

Size Class ($_m$)	Possible Species
> 28m	*Alloeasuarina verticillata*, *Alloeasuarina littoralis*, *A. luehmanii*,
	A. muellerana and
	Alloeasuarina nana
23-27m	*Alloeasuarina paludosa*,
	A. pusilla, Casuarina cristata
<23m	Possibly *C. cristata*?

Table 1.   Subdivision of Casuarinaceae pollen (after of Kershaw, 1970; Dodson, 1974b, 1975)

studies of pollen dispersal in southeast Australia (eg. Hope 1974; Macphail 1979; Dodson 1982/83, Hill & Macphail 1985; Kershaw et al. 1994a; D'Costa & Kershaw 1997), the pollen sum was designed to reflect the regional vegetation and consisted of the following taxa: *Lagarostrobos*, *Phyllocladus*, *Nothofagus cunninghamii*, *Cyathea*, *Dicksonia*, *Eucalyptus*, Casuarinaceae, *Dodonaea*, *Pomaderris*, Gyrostemonaceae, Asteraceae and Poaceae.

For the majority of taxa, identification was restricted to genus or family level. One species of eucalypt was tentatively distinguished (*Eucalyptus spathulata* type) with the remainder being divided into *Eucalyptus* spp. and a large *Angophora* like type (*Eucalyptus/Angophora*). *Melaleuca* was divided into a general species group (*Melaleuca* spp.) and the distinctive *Melaleuca squamea*. Adapting the classifications of Kershaw (1970), Dodson (1974b, 1975) and Edney (1987), three size classes of Casuarinaceae were separated on measurements of the equatorial diameter. These are outlined in Table 1. Two tribes of Asteraceae were recognised: Tubuliflorae and Liguliflorae. The former was subdivided into a type possessing sharp, generally long echinae (type A) and a type with short, blunt echinae (type B) (see Edney 1987). The Asteraceae Liguliflorae identified in the sequence is of the *Taraxacum*-type (see Head 1984; Feuer & Tomb 1977; Wodehouse 1935). *Taraxacum*-type species occurring in Australia today are the introduced species *Taraxacum officinale*, the possibly native *Picris hieracioides* var. *squarrosa* and the native species *Microseris scapigera* and *Taraxacum aristum* (Hnatiuk 1990). In addition to extant mainland taxa, a number of palynomorphs were identi-

fied that are likely to be derived from Tertiary sediments. These include: *Dacrydiumites, Cupanieidites orthotheichus, Nothofagus* subgenus *Brassospora,* and *Nothofagus* subgenus *Fuscaspora*-type

Charcoal was identified as opaque black or dark brown particles with irregular from. It was counted using the Point Count Method of Clark (1982).

The pollen data were expressed as percentages of the pollen sum using the TILIA pollen statistical program (Grimm 1991). TILIAGRAPH (Grimm, 1991) was used to construct the pollen diagrams. Pollen concentrations were calculated against volume of sediment and charcoal was expressed as area per cubic centimetre as well as a ratio of the pollen concentration (based on the pollen sum).

To overcome possible differences in counting techniques and taxon identification, samples used from Edney's (1987) LW84 pollen record were recounted. Unfortunately, Edney (1987) used different methods to those outlined above to determine charcoal and pollen concentrations and the information necessary to recalculate these (eg. volumes of silicon oil added) was not available. Consequently, it was not possible to fill in the gaps in the charcoal and pollen concentration records from core LW87 using data from the LW84 core.

Statistical analyses of the Lake Wangoom pollen data set

Statistical analyses of the dryland taxa were used to identify dryland vegetation *associations* and *assemblages*. The analyses were conducted on a stratigraphically unconstrained data set. The aquatic and ground fern taxa were excluded in order to reduce the impact of local pollen and spore signals.

Following the recommendations of Overpeck et al. (1985) and Prentice (1980), a correlation coefficient method was used for the comparison of the pollen taxa whilst a dissimilarity coefficient approach (using a Manhattan metric) was used to compare the pollen spectra of each of the samples. The data were pre-processed by adding one to the count value and taking the log of the result in order to eliminate problems associated with 0 values as well as increasing, without overweighting, the importance of minor taxa. It should be noted that the associations are based on the strongest alliances rather than all the possible associations, as the

classification technique only allows for a single group allocation of each taxon.

Identification of nearest modern vegetation analogues

Modern analogues in the Southeast Australian Recent Pollen Database (SEAPD) (Kershaw et al. 1994a: D'Costa & Kershaw 1997) were determined for the Lake Wangoom *pollen assemblages* using a dissimilarity coefficient analysis (Prentice 1980; Overpeck et al. 1985; Baker et al. 1989). As with the analyses of the pollen taxa and pollen spectra, the data were log transformed. The modern analogue analysis was based on pollen taxa selected according to the following criteria:

1) presence in both the Lake Wangoom record and the Southeast Australian Recent Pollen Database;

2) representation greater than or equal to 10% in any one sample; and

3) strong association with specific pollen assemblages.

The pollen sum used in the SEAPD (D'Costa & Kershaw 1997) was extended to include *Cyathea* and *Dicksonia,* both of which have widely dispersed spores (Hill & Macphail 1985). Modern sites with significant fluvial input were excluded from the database as fluvial transported pollen is likely to create an over-representation of vegetation communities growing some distance from the site. Following the recommendations of Kershaw et al. (1994a), taxa effectively representing local site communities, such as the aquatic taxa, most fern spores and taxa with poor pollen dispersal (eg. *Melaleuca* and Ericaceae) were omitted. [The family Epacridaceae has recently been included as Styphelioideae within the Ericaceae (Kron et al. 2002)]. This included Apiaceae as many researchers had failed to separate the frequently aquatic *Hydrocotyle* genus from this family. Also excluded were Chenopodiaceae (which is commonly over-represented in saline environments) and taxa with ambiguous or inconsistent identification in the samples contributing to the SEAPD (eg. Apiaceae, Myoporaceae and Gyrostemonaceae). Pollen percentages in the database were subsequently recalculated, using raw data where available.

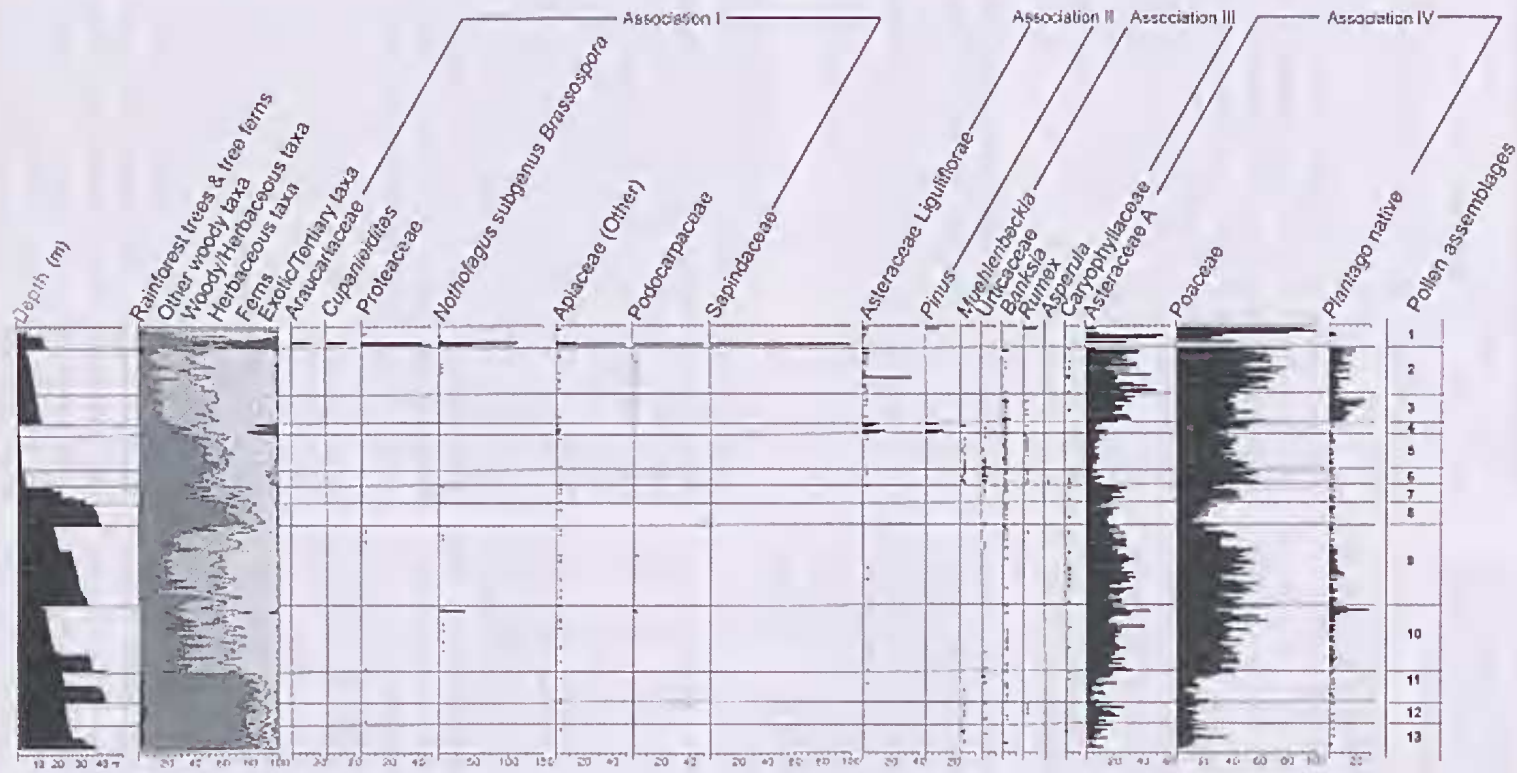In all, the following twenty-one taxa were selected for the modern analogue analysis: *Acacia,*

Figure 2a

Fig. 2. Plot of the dryland pollen associations against the dryland pollen assemblages derived from the stratigraphically unconstrained multivariate analyses of the occurrences of individual pollen taxa and pollen spectra in the Lake Wangoom record. Pollen representation is expressed as percentages of the pollen sum. The graph demonstrates the representation of pollen associations in each pollen assemblage. The depths of the pollen spectra making up each pollen assemblages are plotted against a horizontal axis. See text for further explanation.
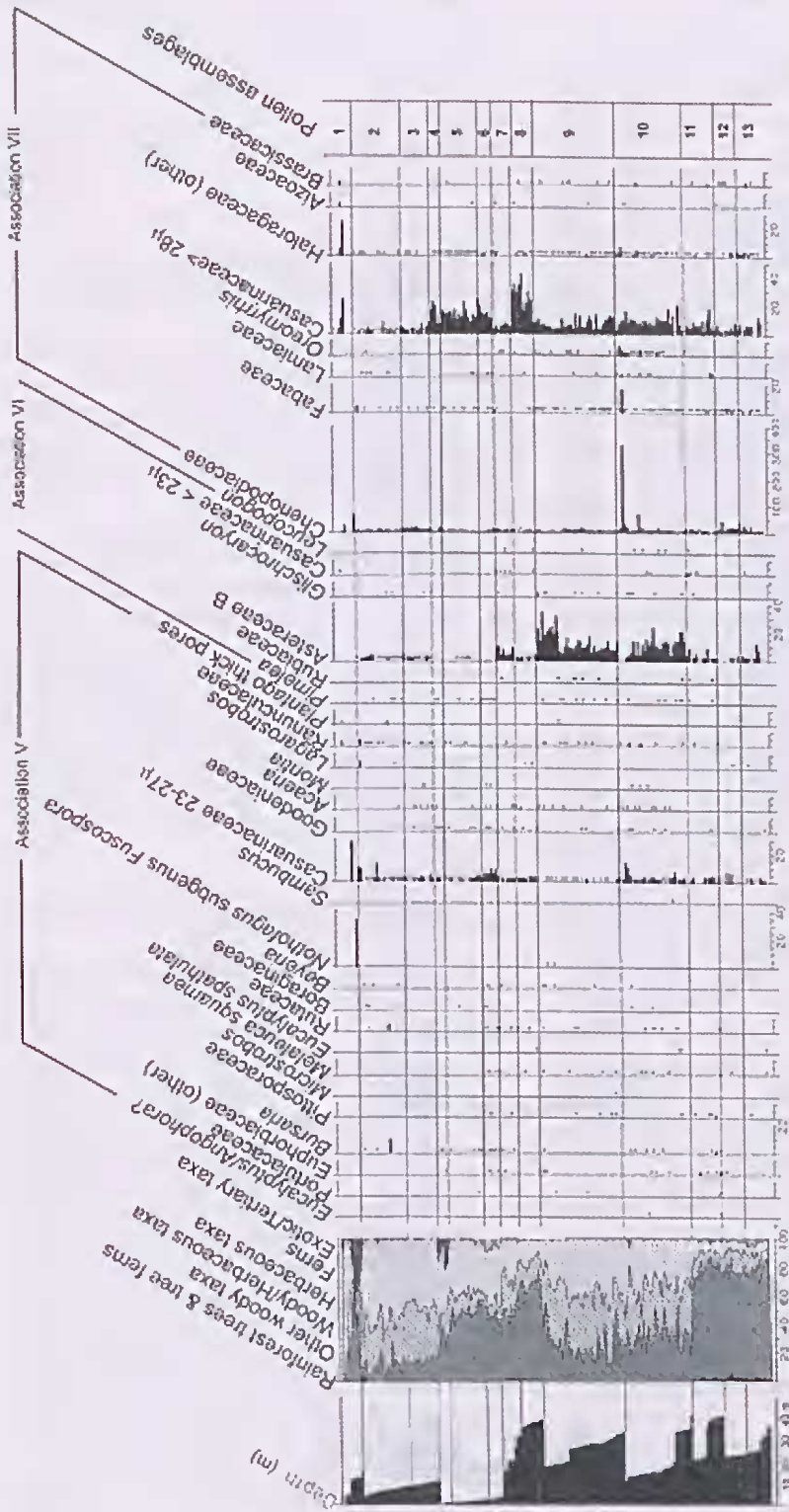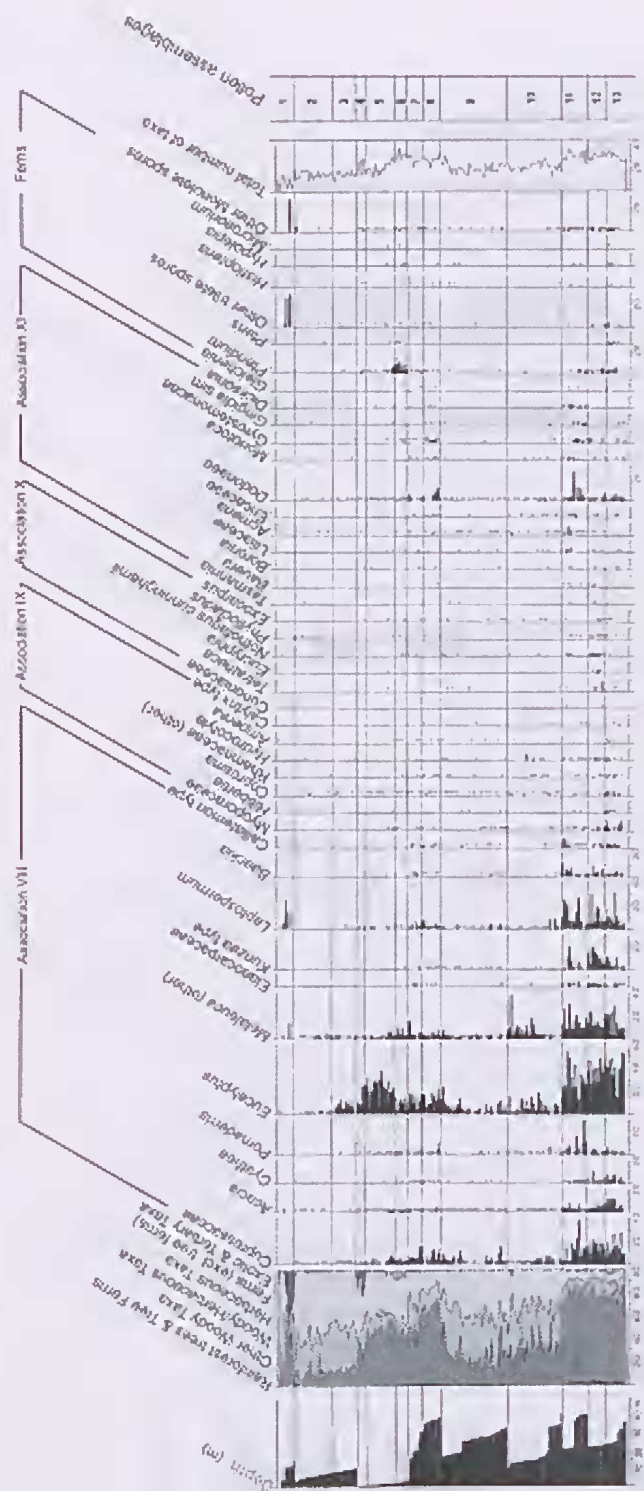
Figure 2b

Figure 2c

Acmena, Asteraceae (Tubuliflorae) type A, Asteraceae (Tubuliflorae) type B, *Banksia, Banera*, Casuarinaeeae, *Coprosma, Dodonaea*, Elaeocarpaceae, *Eucalyptus, Eucryphia, Exocarpos, Nothofagus cunninghamii, Phyllocladus*, native *Plantago*, Poaceae, *Pomaderris, Cyathea, Dicksonia* and *Pteridium*.

RESULTS OF THE STATISTICAL AND MODERN ANALOGUE ANALYSES

Eleven dryland taxon associations and thirteen dryland pollen assemblages were identified from the correlation coefficient analysis of all dryland pollen taxa and the dissimilarity coefficient analyses of the core spectra. These are plotted against each other in Fig. 2.

The nearest modern analogue sites and their surrounding vegetation determined for the pollen spectra in each dryland assemblage are presented in Table 2. For location of these sites see D'Costa and Kershaw (1997). The statistical distances between the pollen spectra in these assemblages and the identified modern analogue sites are given in Fig. 3 according to both sample group and depth. These provide a measure of the dissimilarity between the analogue and the fossil pollen spectra - thus the smaller the distance, the closer the match.

Dryland pollen associations

Dryland pollen association I: This association is composed principally of taxa that have been identified as Tertiary. Araucariaceae, *Nothofagus* subgenus *Brassospora, Cupaneidites* and Podocarpaceae are common in Tertiary sediments from southeast Australia (Cookson 1957; Cookson & Pike 1953,1954; Dettmann et al. 1990; Hekel 1972; Stover & Partridge 1973). The inclusion of Podocarpaceae, Proteaceae and Apiaceae at first appears incongruous. However, all these families have fossil forms in the Tertiary flora: *Podocarpus - Padocarpidites* (Cookson 1947; Hekel 1972) and *Parvisaccites* (Stover & Partridge 1973); Proteaceae - *Proteacidites* (Cookson 1950); and there are many Tertiary tricolporate pollen grains which are similar to modern Apiaceae (eg. *Santalumidites cainozoicus* in Cookson and Pike 1954, Fig. 68, 69, Plate 2).

Dryland pollen association II: Pinus and species of

Asteraceae (Liguliflorae) were introduced to Australia by Europeans. This association appears, therefore, to be determined by the presence of exotic taxa, although there are native species of Asteraceae (Liguliflorae) species also represented.

Dryland pollen association III: All of the taxa represented in this association are native or include native species. Potential source plants are predominantly herbaceous, except for *Banksia* (a small tree or shrub) and *Muehlenbeckia* (a shrub or vine). *Banksia, Asperula* and Caryophyllaceae are widespread through a range of habitats and climates (Costermans 1989; Hnatiuk 1990; Robinson 1997; Walsh & Entwisle 1996). *Urtica* is also found in a range of vegetation communities within the cooler and wetter areas of southeastern Australia (Curtis 1956; Walsh & Entwisle 1996), while *Muehlenbeckia* occurs in woodland and heath communities and on the margins of water courses, swamps and saline lakes (Hnatiuk 1990; Walsh & Entwisle 1996). *Rumex*, which includes exotic species, grows on the margins of water courses, swamps and lakes within temperate regions of southeastern Australia (Hnatiuk 1990; Walsh & Entwisle 1996). Many of the pollen types in this association have poor pollen dispersal and are therefore likely to have been derived from a local source (Dodson 1977; Dodson 1982/83, Hope 1974; Hill & Macphail 1985; Kershaw et al. 1994a; Macphail 1979). It seems probable, especially with the importance of *Banksia* in this group, that this pollen association represents heath (possibly in the understorey of temperate woodland) and lake-side communities growing in and around the Lake Wangoom crater.

Dryland pollen association IV: The three taxa represented in this association (Asteraceae A, Poaceae and the native *Plantago*) are all common in open vegetation communities, such as grasslands and grassy woodlands. Asteraceae type A pollen has a number of additional major sources, including semiarid, coastal and forest communities (Costermans 1989). All three pollen taxa are well to over-represented in pollen surface samples.

Dryland pollen association V: With the exception of Casuarinaceae 23-27m, the taxa in this association all generally have trace to very low percentages. Potential source plants for the Casuarinaceae 23-27m palynomorph include *Allocasuarina paludosa, A. pusilla* and *Casuarina cristata* (Kershaw 1970;

Dryland pollen assemblage	Modern analogue sites	Surrounding vegetation
1	Lake Ranfurlie	- mallee & Casuarinaeeae woodland
	Boomer Swamp	- euealypt woodland
	Bolobek*	- dry selerophyll forest & euealypt woodland
2	Lake Jaka	- Casuarinaceae woodland
	Lake Ranfurlie	- mallee & Casuarinaeeae woodland
	Lake Crosby	- mallee (tall shrubland)
3	Sheet of Water	- dry selerophyll forest & euealypt woodland
	Lake Jaka	- Casuarinaeeae woodland
	Lake Ranfurlie	- mallee & Casuarinaeeae woodland
	Lake Cartearong	- euealypt woodland
4	Sheet of Water	- dry selerophyll forest & euealypt woodland
	Lake Terang	- euealypt woodland
	Lake Gnotuk	- mixed euealypt woodland & grassland
	Boomer Swamp	- euealypt woodland
5	Lake Wangoom	- euealypt woodland
	Sheet of Water	- dry selerophyll forest & euealypt woodland
	Long Swamp	- dry selerophyll forest & euealypt woodland
	Mt Burr	- dry selerophyll forest & euealypt woodland
	Lake Terang	- euealypt woodland
6	Lake Wangoom	- euealypt woodland
	Lake Terang	- euealypt woodland
	Blue Lake (G)	- dry selcrophyll forest & euealypt woodland
	Salt Lake	- dry sclerophyll forest & euealypt woodland
	West Basin	- dry selerophyll & grassland
7	Caledonia Fen	- dry selerophyll forest
	Tiger Snake Swamp	- euealypt woodland
	Lake Terang	- eucalypt woodland
	Egg Lagoon	- wet eoastal serub/heath
	Cobrieo Swamp	- border of dry selerophyll forest & grassland
	Lake Flannigan	- eoastal serub heath

Table 2.   Nearest modern analogue sites for the dryland pollen assemblages based on modern analogue analysis of the pollen spectra. Analogue sites are listed in order of similarity, i.e. closest analogues are listed first. * indicates high dissimilarity (i.e. poor analogue)

Dryland pollen assemblage	Modern analogue sites	Surrounding vegetation
8	Greens bush	- eucalypt woodland
	Lake Terang	- eucalypt woodland
	Long Swamp	- dry sclerophyll forest & eucalypt woodland
	Lake Flannigan	- coastal scrub heath
	Lake Crosby	- mallee (tall shrubland)
9	Lake Crosby	- mallee (tall shrubland)
	Tiger Snake Swamp	- mallee (tall shrubland)
	Caledonia Fen	- dry sclerophyll forest
	Lake Ranfurlie	- mallee & Casuarinaceae woodland
	Lake Lascelles	- eucalypt woodland
10	Lake Crosby	- mallee (tall shrubland)
	Breadlebane NW	- eucalypt woodland
	Lake Jaka	- Casuarinaceae woodland
	Lake Ranfurlie	- mallee & Casuarinaceae woodland
	Sheet of water	- dry sclerophyll forest & eucalypt woodland
11	Lake Curlip	- dry sclerophyll near coastal *Banksia* scrub
	Carlisle State Park	- wet forest & dry sclerophyll
	Lake Lascelles	- mallee (tall shrubland)
	West Basin	- border of dry sclerophyll forest & woodland
	Egg Lagoon	- wet coastal scrub/heath
	Powel Town	- wet forest & dry sclerophyll
12	Lake Tarlikarng	- wet forest, euc. woodland & dry sclerophyll forest
	Lake Flannigan	- coastal scrub heath
	Chappel Vale	- wet forest near dry sclerophyll forest
	Caledonia Fen	- dry sclerophyll forest
	Jacksons Bog B	- grassland & eucalypt woodland
	Lake Terang	- eucalypt woodland
	Lake Curlip	- dry sclerophyll near coast
13	Egg Lagoon	- wet coastal scrub/heath
	Killiecraigie	- wet coastal scrub/heath near wet forest
	Lake Crosby	- mallee (tall shrubland)
	Lake Elusive	- dry sclerophyll forest
	Lake Wangoom	- eucalypt woodland
	Long Swamp	- dry sclerophyll forest & eucalypt woodland

Table 2.   continued

Dodson 1974b, 1975; Edney 1987). *Allocasuarina paludosa* is common in heath and scrub in coastal areas, *A. pusilla* in heath in coastal and drier regions and *C. cristata* in dry inland woodland communities (Costermans 1989; Hnatiuk 1990). Potential source plants for the other pollen taxa included in this association grow in a range of environments, from semi-arid woodland to subalpine (Costermans 1989; Hnatiuk 1990; Walsh & Entwisle 1996). Nearly all of them have representatives in drier woodland, mallee and semi-arid communities. The exceptions are the *Eucalyptus/Angopohora* type (if it is indeed *Angophora*), *Nothofagus fuscospora* type, *Melaleuca squamea*, *Lagarostrobos* and *Microstrobos*. *Angophora* is restricted to dry forest communities, *M. squamea* occurs in heath on damp ground, *Microstrobos* occurs in alpine areas, *Lagarostrobos* occurs in cool temperate rainforest in Tasmania, and the only extant Australia *N. fusca* type is *N. gunnii* - a Tasmanian endemic occurring in wet subalpine communities. It is possible that the *N. fuscospora* type could be reworked Tertiary pollen or, as is potentially the case with *Lagarostrobos*, derived by long distance transport from Tasmania. Given its preference for damp ground, such as occurs in swamps and bogs, it is possible that *M. squamea* was derived from communities within the Wangoom crater.

Although there is a potential range of communities for this association, the dominance of Casuarinaceae 23-27μ suggests the source of much of the pollen may have been open woodland, heath and semi arid shrubland. The possible presence of long-distance dispersed pollen provides support for relatively sparse, open vegetation.

Dryland pollen association VI: Unfortunately the source, and in turn the ecology of the dominant pollen type in this association, Asteraceae B, is unknown. Of the other taxa in this association, *Pimelea* occurs in a range of environments, from wet forest to alpine formations; Rubiaceae (excluding *Asperula*, which is analysed separately) grows in dry forest and coastal scrub and occasionally rainforest; *Glischrocaryon* is restricted to mallee and heath communities; and *Leucopogon* grows predominantly in coastal, dry woodland and mallee communities but can occur in montane forest (Costermans 1989; Hnatiuk 1990). There has been some debate over the source of the Casuarinaceae <23μ pollen type (Singh & Geissler 1985), although Kershaw (1970) speculated it may be derived from *Casuarina cristata*, which grows in semi-arid woodland (Costermans 1989). Overall, the

uncertain source of some taxa combined with the broad geographical spread but limited abundance of other taxa suggests that the assemblage may not be represented in the present landscape. However, the presence of a number of taxa currently growing in drier areas suggests the source community was probably dry.

Dryland pollen association VII: Apart from Casuarinaceae >28μ, Chenopodiaceae and Haloragaceae, the percentages of the taxa included in this association are trace to low. There are a number of Casuarinaceae species in southeastern Australia that have pollen in the > 28μ size class (see Table 1). Of these, *Allocasuarina muellerana* and *A. leuhmannii* occur in heath, mallee and semi-arid woodland in which Chenopodiaceae is a significant component (Costermans 1989). Of the other Casuarinaceae species in this size class, *A. littoralis* and *A. verticillata* grow in coastal to more inland forest, woodland and scrub communities whilst *A. nana* is a sub-alpine species (Costermans 1989). Crowley (1994a) argues that the species generally represented in southern Australian pollen records by Casuarinaceae >28μ pollen is *Allocasuarina verticillata*, which is one of the most salt sensitive species of the family. She suggests that its generally inverse relationship with Chenopodiaceae in these records reflects this salt sensitivity (Crowley 1994a, b). There is some evidence of this inverse trend in many sections of the Lake Wangoom record, particularly in Pollen Assemblages 12 and 13, which are described later. However, Chenopodiaceae and Casuarinaceae exhibit similar trends in representation in Assemblages 1, 9 and 10 (described later), suggesting a salt tolerant source plant. Other taxa in this association (Aizoaceae, Brassicaceae, Fabaceae, Haloragaceae, Lamiaceae and *Oreomyrrhis*) occur in a range of environments, although all are found in mallee and heath communities. Several species also grow in and adjacent to wetlands, with members of the Aizoaceae and Brassicaceae families tolerating fairly saline conditions (Walsh & Entwisle 1996).

Overall, this association most probably incorporates communities of generally dry environments including heath, woodland and perhaps communities growing adjacent to brackish or saline water.

Dryland pollen association VIII: The pollen taxa in this association are all derived from trees and shrubs, most of which have representatives in forest communities. *Eucalyptus* is the dominant taxon in tall
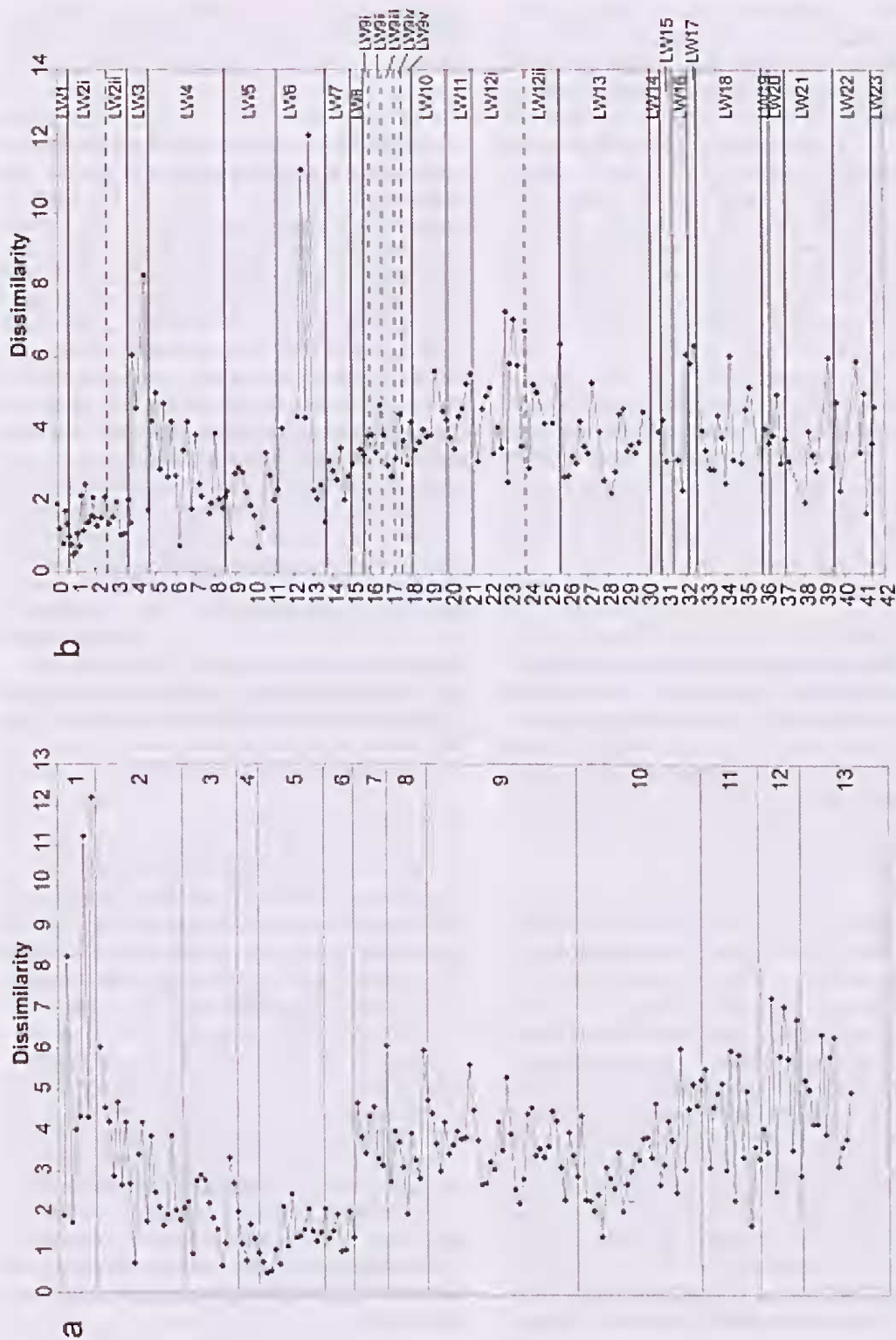
Fig. 3. Dissimilarity curves for the modern vegetation analogues determined for the Lake Wangoom record (a)Dissimilarity for pollen assemblages, which are indicated by numbers 1-13, (b) Dissimilarity vs core depth (m).

shrubland and woodland as well as sclerophyll forest communities throughout southeast Australia, often in association with *Acacia*. *Pomaderris* occurs in both wet sclerophyll and dry sclerophyll forest communities, whilst *Cyathea* and *Elaeocarpus* are restricted to wet forest types. The only native genus of Cupressaceae in Victoria is *Callitris*. It is largely restricted to drier communities, such as open forest and woodlands, although one species, *Callitris rhomboidea*, grows in relatively high rainfall areas along the eastern seaboard and in eastern Tasmania. In western Victoria, *Callitris* is currently restricted to low open forest in the Grampians and in adjacent mallee communities (Costermans 1989). *Callistemon, Leptospermum* and *Melaleuca* frequently fringe water courses and swamps (Costermans 1989) and therefore could be representative of sclerophyll vegetation growing around the margins of Lake Wangoom. *Baeckea* and *Kunzea*, both of which have relatively poor pollen dispersal, could also be part of communities growing within the Wangoom crater.

Dryland pollen association IX: The source plants of most of the pollen taxa in this association are shrubs occurring in heaths, open woodland and scrub on sandy soils, particularly in areas of low rainfall areas and physiological dryness. The exception is the herb *Hydrocotyle*, which although found in a range of vegetation communities, the poor dispersal of its pollen suggests a predominantly local aquatic and/or semi-aquatic (eg. swamp) source.

Dryland pollen association X: With the exceptions of *Tetratheca* and *Exocarpos*, the taxa represented in this association are from wet forest communities, in particular cool temperate rainforest. Two of the taxa (*Eucryphia* and *Phyllocladus*) are no longer extant in Victoria, the latter being confined to temperate rainforest in Tasmania and the former being confined to temperate rainforest in both New South Wales (*Eucryphia moorei*) and Tasmania (*E. lucida* and *E. milliganii*). *Tetratheca* species in western Victoria are small shrubs of dry forest and heath communities (Curtis 1956; Hnatiuk 1990). The parasitic small tree, *Exocarpos*, occurs in dry forest, semi-arid woodland and mallee and as a shrub in subalpine regions of Tasmania and Victoria (Costermans 1989). Overall, this association probably gives evidence of vegetation communities in the wetter southern and

eastern areas of the region and dry sclerophyll forest in inland areas towards the drier end of the rainfall gradient.

Dryland pollen association XI: This association includes species occurring in or marginal to temperate rainforest communities. Several species, such as *Acmena smithii, Boronia muelleri* and *Codonocarpus attenuatus* (Gyrostemonaceae), are now predominantly confined to East Gippsland and coastal NSW, where warm temperate rainforest is found. Indeed, *Acmena* is a frequent dominant canopy taxon of this rainforest type whilst *Dicksonia* is an important component of the understorey (Cameron 1992; Costermans 1989). Codonocarpus also grows in Queensland (Bodkin 1990). Gyrostemonaceae, *Dodonaea, Boronia*, Ericaceae and Liliaceae are recorded in a much wider range of habitats, including semi-arid communities. However, their inclusion in this association strongly suggests that the major occurrence of these palynomorphs within the sequence, particularly where other members of this association also occur, are indicative of more humid communities. Ericaceae and Liliaceae have limited pollen dispersal, so it is likely that they were derived from plant communities, possibly heath and/or bog communities, growing around the margins of Lake Wangoom.

Dryland pollen assemblages

Dryland pollen assemblage 1: The nine samples in this assemblage are characterised by high inter-sample variation, low diversity and frequent dominance by otherwise poorly represented taxa, many of which are considered to be of Tertiary origin or are introduced. Apart from associations I and II, representing the Tertiary and introduced species, there is high representation of associations IV (grassland/herbfield) and VII (open woodland, heath and saline communities). It is considered that this assemblage consists of two sub-assemblages: i) a European modified vegetation with introduced taxa and ii) an assemblage containing a significant proportion of Tertiary pollen flora, most likely reworked from the Tertiary sediments in the Wangoom tuff. The difficulty of separating out reworked pollen significantly reduces the ability to reconstruct prevailing vegetation and climate.

Dryland pollen assemblage 2: This assemblage consists of twenty-one samples from between 380 and 850 cm. They are dominated by taxa in dryland pollen association IV (Asteraceae A, Poaceae and the native *Plantago* type), which are considered to represent grassland and herbfield communities. Consistent with this is the continuous presence of Asteraceae (Liguliflorae), which, given the lack of introduced taxa in this assemblage, is most likely either *Microseris scapigera* and/or *Taraxacum aristum,* both being common in grassland and herbfield communities (Scarlett et al. 1993). The representation of arboreal taxa is the lowest for the diagram, with only minor presence of trees and shrub pollen, predominantly from dryland pollen associations V, VII (open woodland, heath and saline communities) and VIII (sclerophyll forest/woodland). The sporadic trace presence of rainforest trees and tree ferns would most likely have been from long distance dispersal with their representation facilitated by the comparatively open nature of the regional vegetation. Trace percentages of *Nothofagus* subgenus *Brassospora* and Podocarpaceae in three samples are probably derived from minor erosion of Tertiary sediments from the Wangoom crater.

The dominance of this pollen assemblage by dryland pollen association IV coupled with the minimal occurrence of taxa from other associations, in particular the forest associations (associations VIII, X and XI), is consistent with the occurrence of extensive grassland/steppe and herbfield communities. Sparse arboreal cover (less than 10%) is indicated, which in turn suggests the presence of very open woodland and/or shrubland communities. Some support for this interpretation is provided by the modern analogue analysis which suggests the presence of open Casuarinaceae woodland and tall eucalypt shrubland (Table 2).

Dryland pollen assemblage 3: This assemblage, which includes thirteen samples from 860 to 1100 cm, is dominated by dryland pollen association IV, indicating a significant presence of grassland/steppe and possibly herbfield. It is very similar to pollen assemblage 2, although differs in having a higher proportion of *Eucalyptus* and Chenopodiaceae, a lower representation of Poaceae and a slightly different array of minor taxa. The greater proportion of *Eucalyptus* suggests a denser arboreal cover than in assemblage 2, although still low at less than 30%. Chenopodiaceae may have been derived from semi-

arid communities, coastal communities or saltmarsh growing within the Wangoom crater. The lower values of Poaceae may represent a real reduction in the landscape and/or may simply be an artefact of its proportional pollen representation being affected by the rise in other taxa, eg. *Eucalyptus.*

The nearest modern analogues for this assemblage are sites in mixed dry sclerophyll forest and eucalypt woodland, eucalypt woodland and shrubland, and Casuarinaceae woodland (Table 2). It is most likely that this assemblage represents a mosaic of grassland/steppe and eucalypt and Casuarinaceae woodland and shrubland.

Dryland pollen assemblage 4: This assemblage, which incorporates samples from 10 to 60 cm, is dominated by dryland pollen association II, indicating the presence of exotic plants. Also important is dryland pollen association IV, with moderate to high percentages of Poaceae. Values of between 10 and 25 % for *Eucalyptus* and Casuarinaceae >28µ suggest they have some importance, although representation of other arboreal associations, in particular the forest associations (X and XI) is minimal. Trace percentages of *Acacia, Banksia, Leptospermum* and *Melaleuca,* all of which have poor pollen dispersal capabilities, suggest they occurred within the Wangoom crater.

Overall, this assemblage is indicative of vegetation modified by Europeans, with the presence of introduced taxa and a mosaic of open eucalypt and Casuarinaceae woodland and widespread grasslands. This reconstruction is supported to some degree by the modern analogue analysis, which suggests the occurrence of a mixture of eucalypt woodland and dry sclerophyll forest (Table 2).

Dryland pollen assemblage 5: Samples from 70 to 240 cm are included in this assemblage. They are dominated by *Eucalyptus* and Poaceae and to a lesser extent Casuarinaceae >28µ. The three most important pollen associations are III (heath and lake margin communities), VIII (sclerophyll forest components) and IV (grassland/steppe), although the latter is really only represented by Poaceae with consistently low values of Asteraceae A and native *Plantago.*

As with assemblage 4, the existence of open woodlands with grassy understoreys is implied. The moderately high percentages of *Eucalyptus* and the

consistent representation of other taxa from dryland pollen association VIII suggest that eucalypt forest may also have been present. Corroboration is provided by the closest modern analogues, which occur in eucalypt woodland, dry sclerophyll forest and in mixed eucalypt woodland/grassland communities. Low dissimilarity values indicate that these are close analogues (Fig. 3).

The continuous presence of pollen association III suggests heath/wetland communities may have existed around the site, with *Banksia, Muehlenbeckia, Rumex* and minor occurrences of *Urtica* and perhaps *Melaleuca* and *Leptospermum*.

Dryland pollen assemblage 6. Incorporating seven samples between 260 and 370 cm, the palynoflora of this assemblage is similar to that of Assemblage 4. It is dominated by Poaceae, has low to moderate percentages of *Eucalyptus* and Casuarinaceae >28µ, low but consistent representation of Asteraceae A and Chenopodiaceae and an absence of Asteraceae B. The major differences from assemblage 4 include the absence of exotic pollen association II, a more consistent representation of taxa from dryland pollen association III (heath and lake margin communities) and higher, more consistent representation of dryland pollen assemblage VIII (sclerophyll forest) in particular Cupressaceae, *Pomaderris, Melaleuca,* as well as ferns, especially *Pteridium*.

This assemblage appears to represent a mosaic of vegetation types including woodland (dominated by *Eucalyptus,* Casuarinaceae and Cupressaceae), grassland (including as understorey to open woodland), dry sclerophyll forest and a relatively well developed swamp around the margins of Lake Wangoom. The closest modern analogues occur within woodland and dry sclerophyll communities (Table 2).

Dryland pollen assemblage 7. This assemblage includes eight samples from a variety of depths (1640, 1660, 2020-2060, 2700, 3160 and 3200 cm). Dryland pollen association IV (grassland/steppe) is the best represented with moderate percentages of Asteraceae A and Poaceae. Dryland pollen association VIII (sclerophyll forest/woodland) is of some significance, with moderate to low values of Cupressaceae, *Eucalyptus, Leptospermum* and *Melaleuca* and the low but consistent presence of *Acacia, Baeckea, Callistemon,. Cyathea* and *Pomaderris*. Also impor-

tant are Asteraceae B (pollen association VI), which has moderate percentages, and the low but continuous presence of *Pteridium*. The overall representation of arboreal taxa is moderately high, principally due to the number of arboreal taxa present rather than large percentages of any one type. The lack of any clear dominant taxa or community types suggests that the regional vegetation was composed of a mosaic of types, including dry sclerophyll forest (dominated by *Eucalyptus* and perhaps), open *Eucalyptus* and Casuarinaceae woodland, grassland, herbfield and some minor occurrences of wet sclerophyll (indicated by the presence of wet forest taxa such as *Pomaderris* and *Cyathea*). This mixed pattern of vegetation is certainly apparent in the modern analogue analysis, with closest analogues including wet coastal scrub/heath, tall shrubland (mallee), eucalypt woodland and dry sclerophyll forest (Table 2).

Dryland pollen assemblage 8. Dryland pollen assemblage 8 is composed of ten samples close to the base of the core (3580, 3600, 3700-3860, 3940, 3960 cm). It is dominated by Casuarinaceae >28µ (dryland association VII - dry heath/woodland), which has its highest percentages for the sequence, although other taxa from this association are not well represented. Dryland pollen association VIII (sclerophyll forest/ woodland) has some importance, with moderate percentages of Cupressaceae and *Eucalyptus* and consistent but low values of *Acacia, Leptospermum, Melaleuca, Pomaderris, Cyathea* and *Kunzea*. Dryland pollen association XI (wet forest/temperate rainforest) is moderately well represented. There is some presence of dryland pollen association IV (grassland/steppe), with moderate percentages of Asteraceae A, moderate to low values of Poaceae and low values of the native *Plantago*. Overall, the herbaceous taxa are relatively poorly represented.

The dominance of this assemblage by Casuarinaceae >28 µ pollen suggests the widespread occurrence of Casuarinaceae (most probably *Allocasuarina verticillata*) woodland and/or forest. *Eucalyptus* and Cupressaceae may have been subdominants or could have formed more restricted occurrences of other woodland and forest types.

The proportionally high percentages of *Dodonaea* and Gyrostemonaceae may have been derived from relatively dry communities, such as semi-arid woodland or heath. However, the presence of other taxa from pollen association XI suggests that their source was wet forest possibly marginal to temperate rain-

forest. Indeed, the presence of wet forest components from dryland pollen associations VIII, X and XI (eg. *Cyathea, Elaeocarpaceae, Pomaderris, Acmena and Phyllocladus*) indicate that small patches of wet sclerophyll and perhaps rainforest communities occurred within the region.

The closest modern analogues (Table 2) exhibit a moderately high dissimilarity to this assemblage. The analogues selected by the analysis consist of a mix of eucalypt woodland, dry sclerophyll forest, coast scrub/heath and mallee shrubland. The latter were probably selected because of their reasonably important Casuarinaceae component.

Dryland pollen assemblage 9. This assemblage includes thirty-six samples between 1740 and 3360 cm. It is dominated by dryland association IV (grassland/steppe) and Asteraceae B (pollen association VI). There are moderate percentages of taxa from dryland association VII (dry heath/woodland). Taxa from the dryland pollen associations indicative of forest communities have low to trace representation. Casuarinaceae >28µ is the best represented of the arboreal taxa, with moderate percentages. Cupressaceae representation ranges from moderate to absent, whilst *Eucalyptus* percentages are generally low. There is an array of other trees and shrubs, such as *Acacia, Banksia, Baeckea, Kunzea, Leptospermum* and *Dodonaea*, but all with very low to trace values.

The palynoflora of this assemblage indicates the widespread occurrence of grassland/steppe and herbfield communities. The presence of *Acaena* suggests that some at least of this grassland was temperate rather than semi-arid. The presence of open woodland, mainly Casuarinaceae dominated, and some heath is also implied. Trace percentages of wet forest taxa, such as *Cyathea*, may have been derived from small isolated patches of wet forest communities in the region, although probably some distance from the study site. It is a pity that the ecology of Asteraceae B is unknown, as its high percentages in this assemblage indicates that it was a significant component of the landscape.

The modern analogues analysis indicates a range of open forest, woodland and shrubland communities, including mallee, Casuarinaceae and eucalypt woodland and to a lesser degree dry sclerophyll forest (Table 2).

Dryland pollen assemblage 10. Thirty samples, ranging in depth from 1120 cm to 4150 cm, are included in this assemblage. Overall, it is very similar to dryland pollen assemblage 9, being dominated by the herbaceous and woody/herbaceous taxa, in particular dryland pollen association IV (grassland/steppe), Asteraceae B and Chenopodiaceae. However, it has a higher representation of pollen associations V and VI as well as *Eucalyptus* (slightly), *Melaleuca, Oreomyrrhis* and Chenopodiaceae. It also includes two taxa from dryland pollen association I (*Nothofagus* subgenus Brassospora and Podocarpaceae), suggesting some possible minor contamination by Tertiary sediments.

This assemblage indicates a regional vegetation composed largely of grassland/steppe, herbfield and dry heath with scattered stands of scrub and woodland in more sheltered and higher rainfall areas. The drier communities are implied by the combination of reasonably high percentages of Casuarinaceae 23-27µ and Chenopodiaceae together with the presence of a suite of taxa found in semi-arid environments, such as *Beyeria, Bursaria, Leucopogon, Boraginaceae* and *Glisclrocaryon. Melaleuca* may also have been derived from such communities. The modern analogue analysis provides support for the presence of dry communities, with analogues generally consisting of open and semi-arid woodland and shrubland (Table 2). Heath communities are likely to have included *Banksia*, Rhamnaceae and perhaps *Hydrocotyle* and *Oreomyrrhis*.

Dryland pollen assemblage 11. Incorporating fourteen samples from between 2080 and 4140 cm, this assemblage is dominated by arboreal taxa, in particular those in dryland association VIII (sclerophyll forest/woodland). Also important are taxa from dryland pollen association XI (wet forest, especially warm temperate), with the highest percentages in the sequence of *Acmena* and *Dicksonia*. There are trace to low percentages of most taxa from dryland pollen associations IX (heath/woodland shrubs) and X (wet forest, especially cool temperate), including *Nothofagus cunninghamii* and *Phyllocladus*. The woody/herbaceous and herbaceous taxa are poorly represented, with very low percentages of Asteraceae, Poaceae and the native *Plantago*.

The dominance of this assemblage by dryland pollen association VIII implies eucalypt forest was widespread, with much higher proportions of Cupressaceae and *Acacia* than is evident today. High

percentages of *Pomaderris* coupled with the presence of other wet forest components, such as the tree ferns (*Cyathea* and *Dicksonia*), indicate that a significant component of the eucalypt forest was wet sclerophyll forest. Low but consistent percentages of rainforest trees (eg. *Nothofagus cunninghamii* and *Phyllocladus*) and the presence of taxa in dryland pollen association XI strongly suggests that stands of cool temperate rainforest and elements of warm temperate rainforest also existed in the region. It is not clear whether the latter actually formed communities of warm temperate rainforest or were merely relict components within other wet forest communities, such as cool temperate rainforest.

Support for forest domination, including the occurrence of wetter forest types, is provided by the closest modern analogues, which include both wet and dry sclerophyll communities (Table 2).

The sources of the high percentages of *Leptospermum* and *Melaleuca* are likely to have been heath and shrubland in the Wangoom crater. Such communities may also have included other Myrtaceae (eg. *Baeckea* and *Kunzea*) and various heath species (eg. Ericaceae and *Monotoca*). The ferns, with the possible exception of *Pteridium*, which may have been widespread in the understorey of open forest and woodland communities, were also likely to have been local.

Dryland pollen assemblage 12. This assemblage covers a continuous sequence of samples from 2220 to 2380 cm. It is very similar to dryland pollen assemblage 11 in that it is dominated by arboreal taxa, in particular those occurring in dryland pollen association VIII (sclerophyll forest/woodland). However, it has a higher representation of Asteraceae A, Chenopodiaceae, *Kunzea* and taxa from dryland pollen association (X). It also has a lower representation of Casuarinaceae, Asteraceae B, *Pomaderris* and taxa from dryland pollen association XI, most significantly *Acmena*, *Dodonaea* and *Dicksonia* (the latter being absent). This assemblage has a greater presence of cool temperate rainforest than in assemblage 11 with a much reduced occurrence of warm temperate rainforest components. The widespread occurrence of wet sclerophyll and some dry sclerophyll forest is also implied, perhaps with some occurrence of woodland communities.

As in dryland pollen assemblage 11, the source of high percentages of *Melaleuca, Leptospermum* and other myrtaceous and heath taxa may have been heath

and scrub communities occurring within the Wangoom crater. The reduced representation of Asteraceae B within this assemblage suggests that environmental conditions suitable for the expansion of cool temperate rainforest were detrimental for the source species of this palynomorph. The overall impression of a mosaic of wet and dry forest communities and woodland is reflected in the closest modern analogues (Table 2).

Dryland pollen assemblage 13. Eleven samples, from a range of depths between 2400 and 3640 cm, make up this final assemblage. As with the previous two assemblages, *Eucalyptus* and other taxa in dryland pollen association VIII (sclerophyll forest/woodland) are dominant. The highest values for *Acacia* and *Eucalyptus* are recorded. Taxa in dryland pollen association IX (heath/woodland shrubs) are also well represented. There are markedly lower values, however, of rainforest taxa. Dryland pollen association IV (grassland/steppe), Casuarinaceae and Chenopodiaceae have moderately low percentages.

This pollen assemblage indicates eucalypt forest dominated the region, a significant proportion of which was likely to have been wet sclerophyll. High percentages of Cupressaceae suggest it was also important, most likely as a co-dominant with *Eucalyptus* in forest and woodland communities. Some presence of dry sclerophyll forest is suggested by the moderately high values of *Pteridium*. The presence of woodland, heath and scrub communities are also implied, particularly by the high percentages of *Melaleuca, Leptospermum* and taxa in dryland pollen association IX. The relatively high influence of scrub and heath communities probably reflects the vegetation within the Wangoom basin. General support for this pattern of regional vegetation is provided by the closest modern analogues (Table 2).

RECONSTRUCTION OF THE LATE QUATERNARY VEGETATION AND ENVIRONMENTS OF WESTERN VICTORIA FROM THE COMPOSITE LAKE WANGOOM RECORD

The composite Lake Wangoom dryland pollen record is plotted against core depth in Fig. 4. It has been zoned with the assistance of the results from the dissimilarity coefficient analysis of the pollen samples. Biostratigraphic zones implied by the pollen assem-

blages were ignored where they involved the isolation of an individual sample. The main assemblage(s) represented in each zone are plotted along with the ferns, total percentage of aquatic taxa, pollen concentrations, area of charcoal, ratio of charcoal to pollen concentration and radiometric dates acquired for the sequence to assist interpretation and establishment of the chronology. Where possible, the zones have been related tentatively to the marine isotope stratigraphy of Martinson et al. (1987).

Interpretation of the charcoal record

Interpretation of charcoal evidence can be problematic as no direct relationship between vegetation, fire and the charcoal produced by it has been established (Clark 1982; McKenzie 1989; Winkler 1985). Expression of the area of charcoal as a ratio of the pollen concentration potentially reduces variables associated with sediment accumulation rates and sediment compression. It is more difficult, however, to assess variation in the influx of charcoal into a closed basin caused by the filtering effect of local vegetation. Examination of the Lake Wangoom charcoal record (Fig. 4) reveals that through most of the record, the highest raw charcoal concentrations are associated with the lowest representation of aquatic taxa. There is a visible reduction in the area of charcoal at the beginning of zone LW 14 in association with a sharp increase in percentage representation of aquatic taxa. This strongly suggests that the presence of aquatic vegetation in the lake had a filtering effect on the quantity of charcoal deposited in the lake sediments and hence in the core. For this record, therefore, high charcoal concentrations will only be taken as evidence of increased fire frequency or intensity where they are obviously not influenced by aquatic plant representation of changes in particle concentration.

Zone LW23. Consisting of a single sample from the base of the core (4150 cm), this zone is quite distinct from those above both on a palynological and sedimentalogical basis. The sharp sedimentary boundary between this sample and the one above raises the possibility of a hiatus. It is therefore difficult to place an age on the sample.

The pollen of this sample falls into dryland pollen assemblage 10 and together with the closest analogues, suggests the regional vegetation consisted of a mosaic of grassland, Casuarinaceae woodland, open shrubland and a limited extent of open eucalypt woodland. Conditions, therefore, appear to have been drier than today. Moderately high charcoal values (very high when expressed as a ratio to pollen concentration) provide evidence for fire in the region.

Zones LW22-19 (The Penultimate Interglacial). Uranium/thorium disequilibrium (UTD) dates and sustained high arboreal representation suggest that zones LW22 to LW19 occurred during the Penultimate Interglacial. Overall, this period is characterised by the presence of rainforest trees, tree ferns and ground ferns, high values of trees and shrubs and low representation of woody/herbaceous and herbaceous taxa. The regional vegetation appears to have been dominated by forest and woodland communities, with a significant presence of wetter forest types. However, the composition of the forest varied throughout the period, with alternating dominance of Pollen Assemblages 11, 8 and 13.

Zone LW22, dominated by Pollen Assemblage 11, indicates the widespread occurrence of wet sclerophyll and dry sclerophyll forest as well as temperate woodland, with Cupressaceae (likely to be Callitris) as well as Eucalyptus forming the canopy. There is some hint of the presence of remnants of warm temperate rainforest with the occurrence of Pollen Association XI. There may also have been very minor occurrences of cool temperate rainforest. Both of these rainforest types may have grown in sheltered locations, probably within the Otway Ranges. Leptospermum and Melaleuca heath and scrub communities most likely grew within and around the Wangoom crater.

Pollen Assemblage 8 dominates zone LW21, indicating that the regional vegetation became more open, with Casuarinaceae (probably Allocasuarina) open forest and/or woodland largely replacing Eucalyptus and Cupressaceae (most likely Callitris) forest communities. Some trace presence of wet sclerophyll forest and rainforest is indicated. The lack of good modern analogues for this assemblage implies that the vegetation landscape was rather different to any extant in the region.

Zone LW20 shows a return to vegetation similar to that in zone LW22, although evidence for wet sclerophyll forest is reduced with lower values of Pomaderris. In contrast to zone LW22, where Eucalyptus gives way to Cupressaceae, Cupressaceae is prominent early, with Eucalyptus becoming dominant in the latter stages.

The return to dominance in zone LW19 of Pollen Assemblage 8 indicates the return to the more open, Casuarinaceae dominated vegetation present during the period represented by zone LW21.

The shifts in vegetation evident during the Penultimate Interglacial were most likely caused by fluctuations in climate, in particular effective precipitation. The transition from the dominance of wet sclerophyll and dry sclerophyll forest in zone LW22 to more open Casuarinaceae dominated forest and woodland in zone LW21 implies a decrease in effective precipitation. The reverse is suggested with the re-expansion of wetter forest types in zone LW20. Effective precipitation then appears to have decreased again with the re-emergence of Casuarinaceae dominated communities at the expense of *Eucalyptus* and Cupressaceae (probably *Callitris*) dominated communities in zone LW19. These apparent climatic shifts do not seem to have substantially affected the incidence or intensity of fire in the region, as revealed by the consistently low charcoal to pollen ratio. Given this low ratio, the moderately high and variable charcoal values are likely to be the product of particle concentration in a deep water lake rather than any significant burning in the region.

Zones LW18-13 (The Penultimate Glacial). There appear to be three major phases within this period – two indicating very open canopied vegetation separated by a middle phase with fluctuation between woodland and forest communities and drier more open canopied vegetation. The earliest phase, zone LW18, is dominated by Pollen Assemblages 9 and 10, indicating the widespread expansion of grassland and herbfield, as well as dry open woodland, shrubland and heath, most probably in response to a decrease in annual effective precipitation. The communities containing woody taxa were dominated by Casuarinaceae (at least two species) with *Eucalyptus* and Cupressaceae (*Callitris*) possibly in areas of slightly higher annual effective precipitation. Small, isolated stands of dry sclerophyll forest may also have occurred in higher rainfall areas, such as the slopes of the Otway Ranges. Asteraceae B is significant in both these assemblages. However, the lack of knowledge about its source prevents interpretation of its ecological or climatic significance. Slightly elevated charcoal to pollen ratios during this phase suggest a higher incidence and/or intensity of fire in the region than experienced during the Penultimate Interglacial.

The second phase is identified by dramatic and short-term fluctuations of Pollen Assemblages 13, 7 and 9. The stratigraphy suggests a fairly rapid and marked regional expansion in zone LW17 of *Eucalyptus* and Cupressaceae (likely *Callitris*) dominated forest and woodland communities, including a minor component of wet sclerophyll forest (Pollen Assemblage 13). This was followed by an opening up of the regional vegetation in zone LW16, with the expansion of grassland and herbfield, either as understorey in woodland and scrub and/or as discrete communities (Pollen Assemblage 7). This trend continued into zone LW15, with a return to the open grassland, herbfield, woodland and shrubland communities of zone LW 18 (Pollen Assemblage 9). There appears to have been a brief re-expansion of forest and closed woodland communities (Pollen Assemblage 13) in Zone LW14. However, this evidence is based on one sample and would require analysis of intervening samples in order to confirm it as being a real event, rather than potential contamination. Asteraceae B remained important throughout. Overall, this phase appears to have been one of fluctuating effective precipitation, with an initial rise (zone LW17) followed by a gradual decline (zones LW16 to LW15) and then a possible sharp increase (zone LW14). The charcoal/pollen ratio suggests low levels of burning in the region at a slightly reduced scale than in the previous phase.

The final phase within the Penultimate Glacial, zone LW13, appears to have been a sustained period dominated by Pollen Assemblage 9. The lack of Pollen Assemblage 10, in comparison to zone LW18, suggests a more open regional vegetation, with widespread grassland and herbfield communities and pockets of open woodland in sheltered locations. The latter were dominated by Casuarinaceae, although *Eucalyptus* and Cupressaceae (probably *Callitris*) were also present. As with the previous zones in the Penultimate Glacial, Asteraceae B remained important. The evidence suggests effective precipitation was low. The incidence/intensity of fire in the region during this phase does not appear to have changed much from the low levels recorded in zones LW17 to 14.

Zone LW12 (The Last Interglacial). Based on UTD dates and the significant and sustained dominance of arboreal taxa, zone LW12 is interpreted as spanning the Last Interglacial. Unfortunately the large uncertainties of the UTD dates (see Harle et al. 2002)

prevent a definite assessment of the exact relationship this zone has to marine oxygen isotope stage 5 (OIS 5), in particular the number of substages it includes. The height of the Last Interglacial (corresponding to substage 5e; Martinson et al. 1987) is certainly present. This period is divided into two phases (subzones LW12ii and 12i) based on changes in the nature of arboreal communities represented.

Defined by Pollen Assemblage 13, subzone 12ii represents a phase where increased effective precipitation caused a rapid expansion of forest communities, in particular eucalypt-dominated wet sclerophyll and dry sclerophyll forest with a significant Cupressaceae (most likely *Callitris*) component. Woodland communities are also suggested as being present in the region. Heath and scrub are indicated as being important, with pollen probably being derived mainly from within the Wangoom crater. A peak in the charcoal to pollen concentration ratio in the middle of this phase suggests a short phase of increased frequency in burning. Higher fuel loads associated with the expansion of forest communities may have contributed to this.

Subzone 12i is dominated by dryland pollen assemblages 12 and 11 (the latter towards the top). The former indicates the expansion of cool temperate rainforest in the region whilst the latter suggests a subsequent expansion of warm temperate rainforest elements. Both probably expanded from sheltered moist gullies in the Otway Ranges and perhaps in isolated and sheltered locations along the coast and in river valleys (such as at the Hopkins River). The rainforest expansion, although limited in extent, was probably in response to an increase in effective precipitation, with levels well above those of today. There are also some possible temperature implications for the increase in warm temperate rainforest elements towards the top of the zone. Woodland communities were probably also present, although the lower representation of Pollen Association IX suggests a reduction in heath and scrub components. *Leptospermum* and *Melaleuca* probably continued to dominate the vegetation on the margins of the Wangoom crater. There appears to have been a drop in the level and/or intensity of burning in the region, indicated by the decrease in the area of charcoal and most significantly by the reduced charcoal/pollen ratio.

Zones LW11-3 (The Last Glacial). More open canopied and drier vegetation within zones 11-3 suggest a period of significantly reduced effective precipitation, which most likely equates to the Last Glacial period.

The early part of this period is characterised by reduced effective precipitation, with the expansion in the region of dry sclerophyll forest, eucalypt woodland, scrub and grassland communities (zone LW11, Pollen Assemblage 7). This was followed by the replacement of forest and closed woodland with open grassland, herbfield and scattered semi-arid woodland/scrub (zone LW10, Pollen Assemblage 9). Percentages of Asteraceae B increased during this phase, becoming significant in zone LW10, indicating its importance in the early Last Glacial flora of the region. The local vegetation around Lake Wangoom also appears to have become progressively more open, with lower values for *Melaleuca* and *Leptospermum*. Both charcoal curves suggest that the level of burning in the region remained moderately low.

Some climatic recovery is suggested by the minor re-expansion of woodland and scrub communities at the base of zone LW9. This heralds the commencement of a complex phase (zones LW9 to LW6) where the expansion and contraction of woodland and scrub, and in particular the changing importance of *Eucalyptus*, provides evidence for fluctuations in effective precipitation. This phase is interpreted as an interstadial within the Last Glacial. Open grassland and herbfield, as well the source of the Asteraceae B pollen, appear to have remained widespread throughout the interstadial, whereas the expansion of woodland and scrub communities peaked at the beginning (subzone LW9v). This suggests highest effective precipitation occurred at the beginning of the interstadial. Following this peak, a cyclical trend of expanding and contracting woodland and scrub communities was overlain by an apparent general decline in the representation of arboreal taxa. This pattern is best illustrated by decreasing representation of *Eucalyptus*, with its possible replacement by *Melaleuca* and the source of the Casuarinaceae 23-27m palynomorph (potentially *Allocasuarina paludosa, A. pusilla or Casuarina cristata*). In turn, this implies the expansion of semi-arid communities in response to decreasing effective precipitation. Evidence for two extremely dry episodes (zones LW8 and LW6), separated by a return to slightly wetter conditions (zone LW7), is provided by marked decreases in arboreal taxa and the occurrence of very low pollen concentrations and barren samples. These zones are dominated by Pollen Assemblage 1, suggesting the regional vegetation was

Figure 4a

Fig. 4. The Lake Wangoom percentage pollen diagram against depth. The dates are derived from uranium-thorium disequilibrium ( ) and AMS radiocarbon ( ) analyses (Harle *et al.*, 2002). Taxa are arranged according to their representation in the *dryland pollen associations*.
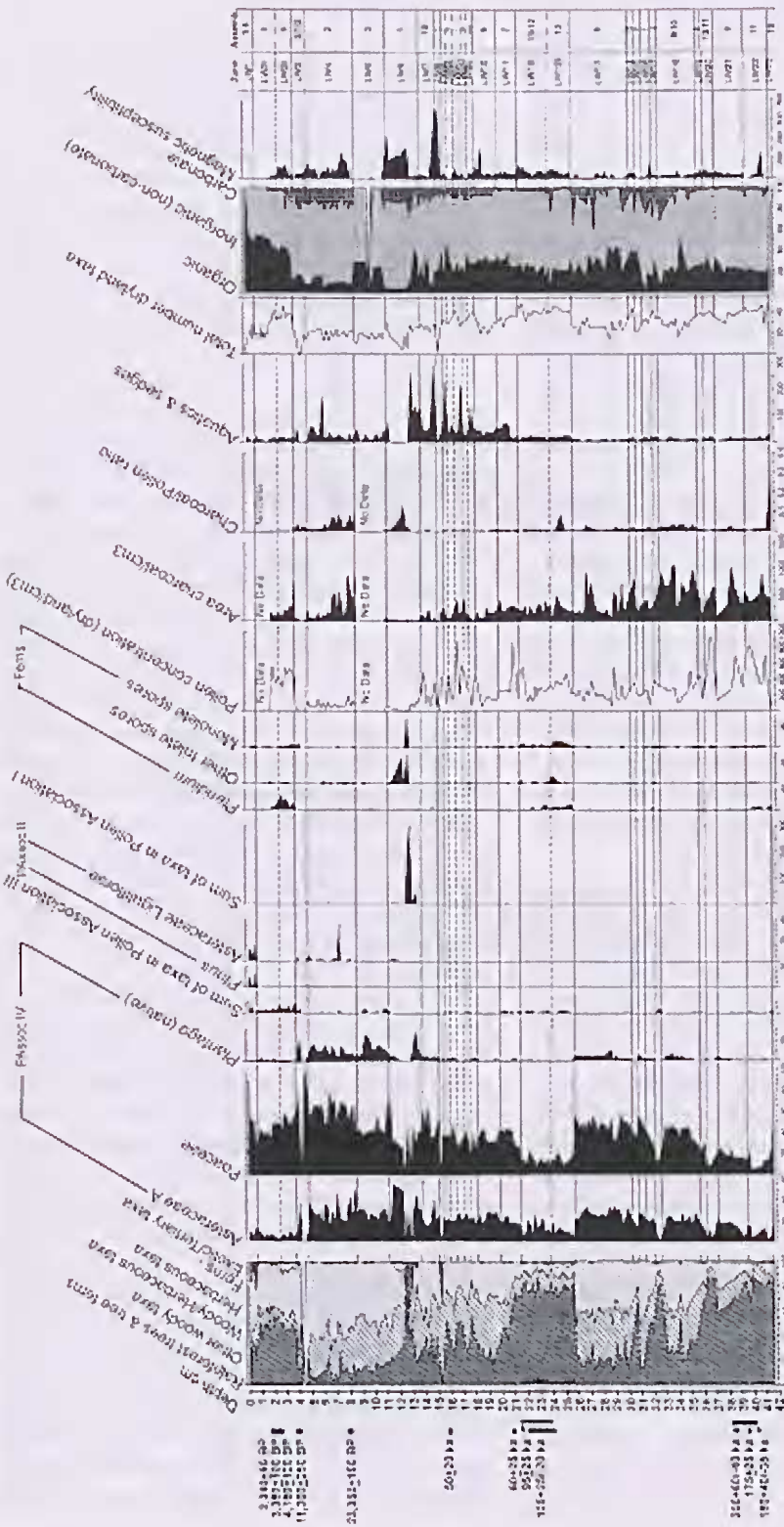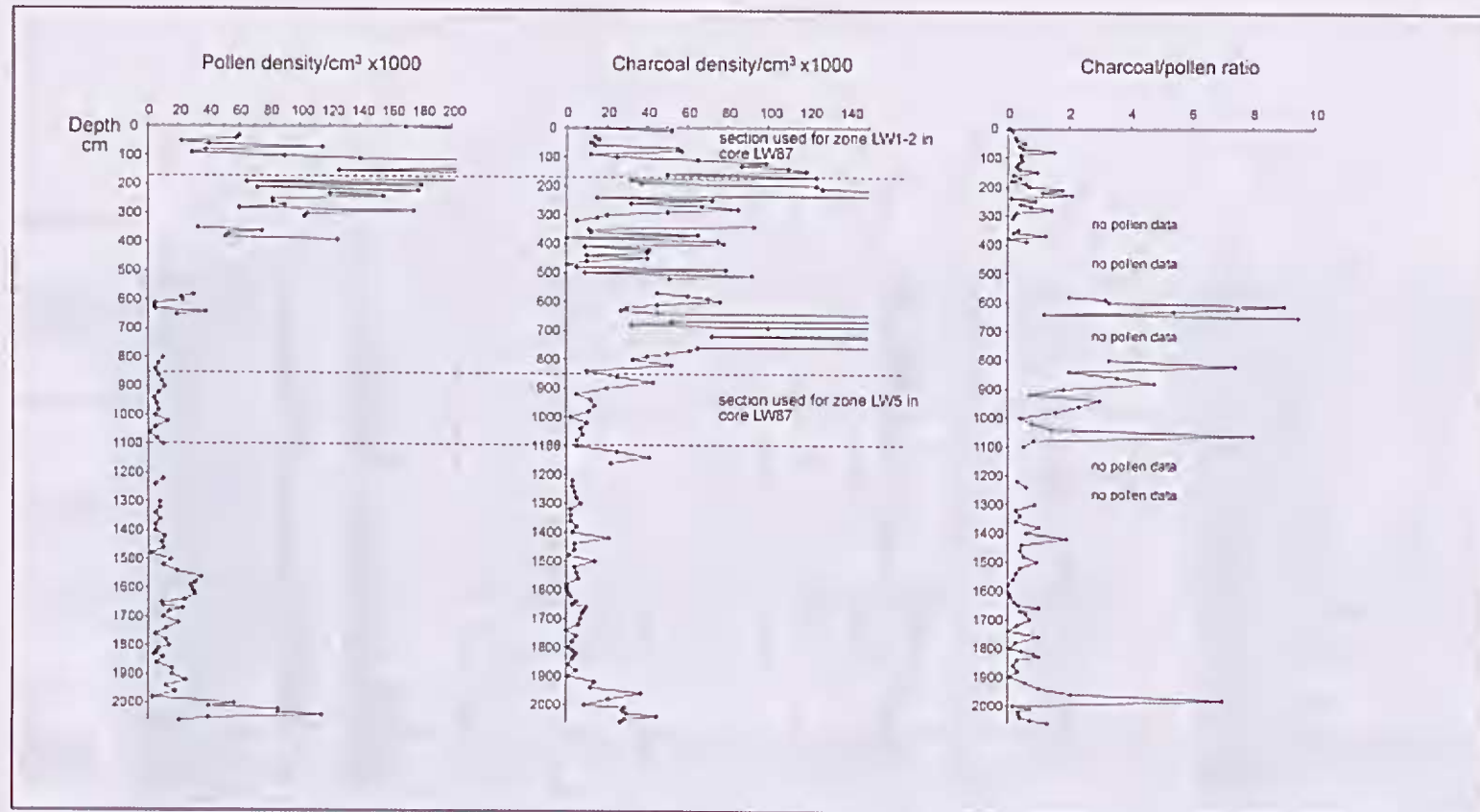
Figure 4b

Fig. 5. Pollen and charcoal density curves from core LW84 as derived from Edney (1987) Figure 6.1. The ratio of charcoal to pollen density is also shown to identify the effects of particle concentration on charcoal representation. The section used from this core to fill gaps in zones LW1, LW2 and LW5 in the LW87 core re bracketed by dashed lines.

composed of a mosaic of open Casuarinaeeae wood-land, serub, heath and steppe. Chenopodiaceae dominated saline wetland communities possibly existed in and around Lake Wangoom. The presenee of Tertiary taxa in this assemblage (including the fern spores) may indieate erosion from the erater rim under a sparse vegetation eover resulting from extremely dry conditions. Support for this interpretation is provided by the high inorganie content and magnetie suseeptibility in these samples (Fig. 4). Alternately, the Tertiary taxa and ash material may aetually have been fallout from nearby voleanie eruptions. One potential souree is the Tower Hill eruption, whieh now has a minimum age of 30 ka (Sherwood et al. this volume). This is younger than the mean 50 ka UTD age determined for sediments within zone LW7 (Harle et al. 2002), although it does fall within its uneertainty range. High ehareoal levels in zone LW6 may also have been derived from voleanie ash, whether from the Wangoom erater or from external sourees. They may also indieate inereased fire frequeney and/or intensity in the region.

Following the arid period of zone LW6, euca-lypt-dominated woodland appears to have onee again expanded (zone LW5), implying a rise in effeetive preeipitation. The dominanee of this zone by Pollen Assemblage 3 suggests the regional vegetation eon-sisted predominantly of open grassland and seattered stands of open euealypt woodland with a grassy understorey. Interestingly, the signifieantly redueed values of Asteraeeae B suggest the souree plant of this palynomorph was no longer an important eom-ponent of the regional flora. Indeed, levels are similar to those reeorded for the previous two interglaeials. The regional vegetation present during this phase appears to have been remarkably different to those of previous periods in the Lake Wangoom reeord. A possible explanation for this is that elimatie eonditions were unique in eomparison to those expe-rieneed previously. However, other faetors also needed to be eonsidered, in partieular the potential influenee of fire. There is evidenee in the previous zone (LW6) for possibly inereased burning in the region, whieh may have eontributed to opening of the regional vegetation. The ehareoal evidenee from the LW84 core (Fig. 5), from whieh data for this seetion was used, also indieates eomparatively higher ehareoal levels during the zone LW5 phase. Data from both the LW84 and LW87 eores indieate that this trend continued into the following phase (zone LW4), eorresponding with evidenee for an even more open eanopied regional vegetation (Pollen Assemblage 2).

The apparently elose assoeiation of higher ehareoal proportions and the presenee of more open plant eom-munities provides support for the argument that in-ereased fire frequeney and/or intensity had a signifi-eant impaet on the regional vegetation from around 50 ka to the end of the Last Glaeial period.

The final phase in the Last Glaeial period (zone LW3) appears to have been extremely dry, with very low pollen eoneentrations (some samples are barren) implying the lake frequently dried up. It is diffieult to determine if this was the most arid period in the reeord, given that Wangoom basin would have been markedly shallower than during the Penultimate Gla-eial due to over 20 m of sediment having been deposited in the intervening time. With a mueh smaller lake eapaeity, the probability of the lake beeoming dry during the late Last Glaeial would have been higher than during the Penultimate Glaeial, when the lake reservoir would have been considerably greater. General shallowing of the lake is supported by the increasing abundance of aquaties through the reeord indieating the expansion of swamp. The palyno-stratigraphy of zone LW3 suggests the regional flora was dominated by open grassland/steppe and herbfield, with seattered oeeurrenee of open semi-arid woodland and serub, dominated by Casuarinaceae (Pollen Assemblages 2 and 3). Over-all arboreal representation is extremely low, with *Eucalyptus* being largely absent.

Zones LW2-1 (The Holocene). A radioearbon age of 11,000±250 BP marks the eommeneement of a dra-matie and apparently rapid expansion of trees in the region, with a mosaic of dry selerophyll forest, *Eu-calyptus,* Casuarinaceae and Cupressaeeae (*Callitris*) woodland and temperate grassland beeoming estab-lished (Pollen Assemblage 6). The latter most prob-ably formed a signifieant eomponent of the understorey of woodland eommunities. Heath may also have been important in the understoreys of for-est and woodland eommunities. It also possibly grew within the Wangoom erater and around the lake mar-gins. This vegetation mosaie was widespread in the region throughout the early to mid Holoeene (Zone LW2ii). The drop in the ratio of ehareoal to pollen eoneentration suggests a reduetion in the level of burning in the region.

A shift in the dominanee of the regional vegeta-tion oeeurred around 4, 000 BP - eueplypt woodland and open forest probably replaeing that dominated by the Casuarinaeeae 23-27m speeies (either

Allocasuarina paludosa, *A. pusilla* or *Casuarina cristata*) and possibly *Melaleuca*. Communities dominated by the source of Casuarinaceae >28m (probably *A. verticillata*) appear to have remained important as does grassland. Unfortunately comparative charcoal data is not available for the whole of this period, due to the use of samples from the LW84 core. Data that is available (Fig. 5) suggests fire was not an important component of the landscape, although little can be said about the period form ca 3,000 BP to the present.

Zone 1 contains clear evidence of the impact of European settlers on the regional vegetation with the establishment of Pollen Assemblages 4 and 1. Widescale clearance of forest and woodland for pasture is evident in the sharp decrease in arboreal pollen percentages and corresponding increase in Poaceae. The reduction in the number of pollen taxa present is testament to the loss of native floristic diversity in the region and the appearance of *Pinus*, *Plantago lanceolata* and Asteraceae Liguliflorae (probably *Taraxacum officinale* and/or *Hypochoeris radicata*) signifies the spread of introduced plants. Low values of Cupressaceae pollen in this zone may be indicative of the presence of the introduced genus *Cupressus*.

DISCUSSION

Multivariate analysis has proved extremely valuable in the interpretation of the Lake Wangoom pollen record. It has allowed the identification of pollen associations and assemblages, including communities like warm temperate rainforest, which would perhaps otherwise have gone unnoticed or their relationships unrecognised. The identified taxon associations for the most part make ecological sense given the present range of potential source plants. However, in a few cases the associations are somewhat puzzling, particularly where they include taxa that appear to be in ecological conflict. In these cases it is likely that a mosaic of vegetation communities are represented, with the common factor being a similar response to climate change or that, due perhaps to extinction at a species level, associations have changed through time. The region incorporates a range of vegetation communities occurring along a distinct climatic gradient from the coast inland. Climate change would result in different responses across this gradient. For example, an increase in effective rainfall would likely cause an expansion of

dry forest in central western Victoria paralleling cool temperate rainforest expansion in the wetter areas around the Otways. This would have been complicated by the role of soils, with spatial differences in soil properties contributing significantly to floristic and structural diversity of vegetation communities within climatic boundaries (Beadle 1981). A further complication would be the response of vegetation communities within the Wangoom crater, particularly in association with the local hydrology. Separating local from regional pollen can at times be an impossible task, particularly in the case of widely dispersed pollen taxa.

In general, the modern analogue analysis supports the multivariate analysis. There is a good match between the closest modern analogues and the dryland pollen assemblages in many parts of the record, with the highest degrees of correlation occurring in dryland pollen assemblages 4, 5 and 6. This is not surprising given that they consist of the most recent samples and hence are most likely to contain vegetation akin to modern communities. Where there is no clear match, the fossil pollen spectra suggest the presence of communities no longer extant in the study region. For example, the modern analogues for most of the samples in dryland pollen assemblage 1 are not particularly close due to the significant proportion of Tertiary pollen they contain. The modern analogues determined for samples in dryland pollen assemblage 8, although much closer and exhibiting the general trends apparent in this assemblage, do not adequately reflect the high proportion of Casuarinaceae, also suggesting that no close modern analogue exists.

Multivariate and modern analogue techniques proved valuable not only in determining the composition of vegetation mosaics growing in the region through the record, but also in identifying repeated occurrences of these mosaics throughout the sequence. From this it was possible to recognise both cyclical as well as long term shifts in vegetation community and species composition in western Victoria over the last 200.000 years. Major, broad-scale changes in the regional vegetation were associated with the cyclical climatic fluctuations driven by global orbital forcing and most clearly reflected in interglacial and glacial periods - the former being characterised by the expansion of woodland and forest communities and the latter by the regional dominance of dry open steppe, herbfield and scrub communities. Superimposed on this is evidence for long term changes in the regional vegetation, with a signifi-

cant reduction in rainforest taxa in the last 100,000 years and a trend to more open vegetation. This is highlighted when a comparison is made between the composition of the forest and woodland communities in each of the three interglacials. Both the Penultimate and Last Interglacials are characterised by a dominance of forest communities (including elements of temperate rainforest) and very restricted representation of grassland. In contrast, the regional vegetation throughout the Holocene was more open, with grassland communities having greater significance and closed forest communities being very limited in their extent. Rainforest and wet sclerophyll understorey taxa appear to have been particularly reduced. Possible reasons for this apparent long term shift towards more open vegetation include: increasing aridity through the Quaternary; long term changes in soil fertility, possibly associated with volcanic activity; and anthropogenic impact.

Several lines of evidence indicate a trend of increasing aridity from the Tertiary through the Quaternary. Lacustrine records suggest lakes became seasonally dry from the mid Miocene (Bowler 1986; Singh et al. 1983), with the establishment of saline, evaporative lakes (playa lakes) between 0.9 and 0.5 Ma (An et al. 1986; Bowler 1982; Bowler & Teller 1986; Chen & Barton 1991). The initiation of dune formation has been dated to between 0.98 and 0.5 Ma (An et al. 1986; Bowler 1982; Chen & Barton 1991) whilst there is a marked rise in aeolian dust content in cores from the Tasman Sea towards the end of the Pleistocene (Hesse 1994). Evidence for vegetation change also appears to support the concept of increasing aridity, with pollen records from Australia demonstrating a shift from closed-canopied rainforest to more open, sclerophyll vegetation (eg. Kershaw 1985; Longmore & Heijnis 1999; Singh & Geissler 1985). This trend appears to have accelerated in the late Tertiary (Kershaw 1988; Kershaw et al. 1994b; Martin 1989, 1990; McEwan-Mason 1991) and continued through the Quaternary, culminating in the reduction and disappearance of rainforest from many regions of Australia towards the end of the Pleistocene (Bohte & Kershaw 1999; Colhoun & van de Ger 1998; Colhoun et al. 1977; Colhoun et al. 1982; D'Costa 1997; Kershaw 1976, 1985, 1993; Kershaw et al. 1993; Longmore 1997; Longmore & Heijnis 1999). In southern Australia, evidence for the local extinction of rainforest taxa includes: the presence of *Nothofagus cunninghamii* (which no longer exists on King Island) in the Egg Lagoon pollen record between 90 and 120 ka (D'Costa 1997);

the disappearance of rainforest taxa in the Lake Terang record from western Victoria after the last major wet phase (D'Costa & Kershaw 1995); and the disappearance of rainforest taxa in the Lake Wangoom record itself. However, maximum rainforest expansion in the Wangoom record occurred during the Last Interglacial, not in the Penultimate Interglacial as would be expected if a long term trend of increasing aridity was the major cause of rainforest extinction in the region. Furthermore, the representation of other key taxa in the sequence do not appear to exhibit any long term trends. For example, values of Casuarinaceae are highest in the Penultimate Interglacial and the Holocene whilst *Eucalyptus* has greatest representation in the Last Interglacial. Indeed, the evidence suggests that of the three interglacials represented in the Lake Wangoom record, the Last Interglacial was the wettest, with the greatest and most sustained expansion of wet forest communities, including wet sclerophyll and temperate rainforest.

Fire has also been invoked as a major factor in the expansion of sclerophyll taxa and demise of rainforest communities, with many records exhibiting a corresponding increase in charcoal content (Kershaw 2002). To what extent this increase in fire was a result of increasing aridity or by the arrival of people on the continent is the subject of much debate. In the Lake Wangoom record, evidence for increased burning in the region between 50 ka and 23 ka is associated with the opening up of the regional vegetation, in particular the expansion of grassland and open woodland communities. The implication is that fire was the cause of this vegetation change. What distinguishes this phase from previous episodes of increased fire in the record, is the higher charcoal/pollen ration, suggesting more extensive and/or more frequent burning, coupled with the significant loss of woody taxa. None of the pre-Last Glacial phases of increased burning appear to be associated with comparable shifts in regional vegetation composition. A charcoal peak early in the Last Interglacial (zone LW12ii) occurs when eucalypt forest was widespread in the region, with no significant vegetation changes before or after. A less pronounced but more sustained phase of burning during the Penultimate Glacial appears to be associated with an expansion of more open vegetation at the expense of woodland and forest communities. However, there was not the same degree of loss of woody taxa as evident during the Last Glacial burning phase. Furthermore, the level of burning appears to have been less during the Pe-

nultimate Glacial, despite the greater abundance of
woody taxa and with it higher available fuel loads.
The elevated levels of burning during both glacial
phases may have been a natural response to the on-
set of more arid conditions. Fire frequency is known
to increase as precipitation decreases, due to the dry-
ing out of fuel sources and subsequent increased flam-
mability (Ashton 1993). Certainly, the rise in char-
coal concentration during the Penultimate Glacial
post-dates the shift in vegetation, suggesting drier
conditions promoted the apparent increase in fire
around this time. Unfortunately the lack of a compa-
rable charcoal record for zone LW5 prevents a simi-
lar assessment of the relationship between timing of
fire and vegetation change during the Last Glacial
burning phase. The apparent differences in burning
levels between the two glacials cannot be explained
by drier conditions, particularly when charcoal lev-
els remained high during the Last Glacial for some
time after the vegetation became very open and fuel
availability would have been reduced. An alterna-
tive explanation for increased burning is that in-
creased volcanic activity in the latter part of the Last
Glacial was responsible, with ignition by eruptions
and lava flows sweeping across an already dry land-
scape. Certainly, elevated magnetic susceptibility
levels (although not as high as in zones LW8 and
LW6) could point to an increased component of vol-
canic ash being deposited in Lake Wangoom. Erup-
tions in the region are dated as occurring during this
period, including Tower Hill (Sherwood et al. this
volume). However, such eruptions were relatively
infrequent relative to climate variation and succes-
sional adjustment to vegetation. They were also spa-
tially scattered, making a substantial impact on the
regional vegetation unlikely. Another potential cause
is the anthropogenic use of fire. It has been argued
(Flood 1995; Jones 1969, 1975; Nicholson 1993;
Tindale 1959) that Aborigines frequently used fire
to aid hunting, promote the growth and regeneration
of economically useful plants and to extend the range
of more open vegetation rich in both faunal and plant
food reserves. Increased levels of burning during the
Last Glacial, therefore, may have been the result of
the implementation of 'fire stick farming' practises
by Aboriginal people. This explanation has been in-
voked for other records where there is evidence of
major shifts in vegetation coinciding with increases
in charcoal concentration (eg. Singh and Geissler,
1985; Kershaw, 1976, 1986; Moss and Kershaw,
2000). Clearly, more refined dating of the burning
increase in relation to proven evidence for the tim-

ing of Aboriginal presence on the continent is needed
before a firmer link can be demonstrated. Whatever
the cause, it is probable that the sustained incidence
of fire in the region during the last Glacial contrib-
uted to the disappearance of temperate rainforest
communities from much of western Victoria and its
current limited distribution to sheltered locations in
the Otway Ranges.

CONCLUSIONS

Together, the use of multivariate and modern ana-
logue techniques have allowed an objective and com-
prehensive reconstruction of vegetation change over
the last 200,000 years in western Victoria from the
Lake Wangoom pollen record. Application of a cor-
relation coefficient analysis to the occurrence of pol-
len taxa throughout the sequence enhanced the rec-
ognition of community types represented, with eleven
pollen associations being identified. Amongst these
is an association including elements of warm tem-
perate rainforest, which does not currently grow in
the region and which has not been identified in other
late Quaternary records from the area. Several taxa
included in this association have a broad ecological
range (eg. Gyrostemonaceae) and without the statis-
tical analysis, would not necessarily have been sus-
pected as being part of a rainforest complex. The use
of a stratigraphically unconstrained dissimilarity co-
efficient technique to compare each pair of pollen
spectra in the sequence enabled thirteen key *pollen
assemblages* to be identified. Each of these assem-
blages consists of a unique combination of *pollen
associations* and represents a mosaic of vegetation
types present in the region at the time of sediment
deposition. In general, these reconstructions are sup-
ported by modern analogue analysis carried out on
each of the pollen assemblages. However, in some
cases the match between the modern analogues and
the reconstructions was poor, implying the presence
of vegetation communities and/or species no longer
extant in the region. An extreme situation occurred
with Tertiary taxa during dry phases in the Last Gla-
cial, most likely indicating erosion of Tertiary mate-
rial from the Wangoom crater, as well as the occur-
rence of Casuarinaceae dominated assemblages dur-
ing the Penultimate Interglacial which appear to have
no modern equivalents in the region. Not unexpect-
edly, the closest correlation between the modern and
fossil spectra occurred toward the top of the record.
  The statistical analyses also improved the recog-

nition of repetition of vegetation mosaics through time. From this it was possible to identify not only vegetation change associated with interglacial-glacial climatic cycles, but also fluctuations within interglacial and glacial periods. Broadly speaking, interglacials were characterised by an expansion of forest communities; glacial periods by the dominance of open semi-arid to arid grassland, herbfield and scrub; and interstadials by the expansion of woodland, grassland and some dry sclerophyll forest. This cyclical pattern appears to have been overlain by a long-term trend towards more open vegetation, with a reduced presence of woody understorey taxa and increased dominance of grassland during the Last Glacial and Holocene periods. There also appears to have been an accompanying demise in the representation of rainforest taxa in the region. Increasing aridity through the Quaternary provides one possible explanation, which is supported by other evidence from the region. However, this is not supported by the evidence for variation between the interglacials in the Lake Wangoom sequence, with the Last Interglacial exhibiting greatest expansion of rainforest and wet sclerophyll taxa and therefore likely to have had highest effective precipitation.

Fire provides an alternative or additional explanation for the opening up of the regional vegetation during the last ca 50 kyrs. Higher relative charcoal concentrations are associated with this apparent shift in vegetation, suggesting that either increased fire frequency and/or intensity during the late Last Glacial and Holocene periods was a major contributing factor. Such a change in fire regime may have been the result of the use of fire by Aborigines, possibly enhanced by increased volcanic activity.

REFERENCES

An, Zhisheng, Bowler, J.M., Opdyke, N.D., Macumber, P.G. & Firman, J., 1986. Palaeomagnetic stratigraphy of Lake Bungunnia: Plio-Pleistocene precursor of aridity in the Murray Basin, Southeastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 54, 219-239.

Ashton, D.H., 1993. Fire in tall open forests (wet sclerophyll forests). In A.M. Gill, R.H. Groves & I.R. Noble, eds, *Fire and the Australian Biota,* 2nd Edition. Australian Academy of Science, Canberra, pp 339-366.

Australian Surveying and Land Information Group,
1990. *Atlas of Australian Resources. Volume 6: Vegetation.* Australian Government Publishing Service, Canberra.

Baker, R.G., van Nest, J. & Woodworth, G., 1989. Dissimilarity coefficients for fossil pollen spectra from Iowa and western Illinois during the last 30,000 years. *Iowa Quaternary Studies Group Contribution no. 27, Palynology,* 13, 63-77.

Bartington, 1983. *Bartington Instruments magnetic Susceptibility Meter User Manual,* 1983. Unpublished instruction manual.

Bodkin, F., 1990. *Encyclopaedia Botanica.* Collins/ Angus & Robertson, North Ryde, 1083 pp.

Bohte, A. & Kershaw, A.P., 1999. Taphonomic influences on the interpretation of the palaeoecological record from Lynch's crater, northeastern Australia. *Quaternary International,* 57/58, 49-60.

Bonwick, J., 1970. *Western Victoria. Its Geography, Geology and Social Condition. The Narrative of an Education Tour in 1857.* First published by Thomas Brown, Geelong, 1858. Heinemann, Australia.

Bowler, J.M., 1982. Aridity in the late Tertiary and Quaternary of Australia. In W.R. Barker & P.J.M. Greenslade, eds, *Evolution of the Flora and Fauna of Arid Australia.* Frewville: Peacik Publications, 35-45.

Bowler, J.M., 1986. Quaternary landform evolution. In *Australia - A geography, Volume 1, The Natural Environment,* D.N. Jeans ed., Sydney University Press, Sydney, 117-147.

Bowler, J.M. & Teller, J.T., 1986. Quaternary evaporites and hydrological changes, Lake Tyrrell, north-west Victoria. *Australian Journal of Earth Sciences,* 33: 45-63.

Cameron, D., 1992. A portrait of Victoria's rainforests: distribution, diversity and definition. In *Victoria's Rainforests: Perspectives on Definition, Classification and Management,* P. Gell & D. Mercer eds, Monash Publications in Geography No. 41, Monash University, 13-96.

Chen, X.Y. & Barton, C.E., 1991. Onset of aridity and dune-building in central Australia: sedimentological and magnetostratigraphic evidence from Lake Amadeus. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 84, 55-73.

Clark, R. L., 1982. Point count estimation of charcoal in pollen preparations and thin sections

of sediments. *Pollen et Spores*, 24: 523-535.

COLHOUN, E.A. & VAN DE GEER, G., 1998. Pollen analysis of 0-20 m at Darwin Crater, western Tasmania, Australia. *IPPCCE Newsletter*, 11: 68-89.

COLHOUN, E.A., VAN DE GEER, G. & MOOK, W.G., 1977. Pulbeena Swamp, northwestern Tasmania: Stratigraphy and pollen analysis. *X INQUA Congress Abstracts*. Birmingham.

COLHOUN, E.A., VAN DE GEER, G. & MOOK, W.G., 1982. Stratigraphy, pollen analysis and palaeoclimatic interpretation of Pulbeena Swamp, northwestern Tasmania. *Quaternary Research*, 18: 108-126.

COOKSON, I.C., 1947. *Proceedings of the Linnean Society of New South Wales*, 72: 207.

COOKSON, I.C., 1950. Fossil pollen grains of proteaceous type from Tertiary deposits in Australia. *Australian Journal of Scientific Research*, B.3:166.

COOKSON, I.C., 1957. On some Australian Tertiary spores and pollen grains that extend the geological and geographical distribution of living genera. *Proceedings of the Royal Society of Victoria*, 69: 41-56.

COOKSON, I.C. & PIKE, K.M., 1953. A contribution to the Tertiary occurrence of the genus *Dacrydium* in the Australian region. *Australian Journal of Botany*, 1(3): 474-484.

COOKSON, I.C. & PIKE, K.M., 1954. Some dicotyledonous pollen types from Cainozoic deposits in the Australian region. *Australian Journal of Botany*, 2(2): 197-219.

COSTERMANS, L., 1989. *Native Trees and Shrubs of South-eastern Australia*. Weldon Publishing, Sydney, 422 pp.

CURTIS, W.M., 1956. *Student's Guide to the Flora of Tasmania*. Volume 1. L.G. Shane, Government Printer, Hobart, 234 pp.

CROWLEY, G.M., 1994a. Quaternary soil salinity events and Australian vegetation history. *Quaternary Science Reviews*, 13: 15-22.

CROWLEY, G.M., 1994b. Groundwater rise, soil salinization and the decline of *Casuarina* in southeastern Australia during the late Quaternary. *Australian Journal of Ecology*, 19: 417-424.

CROWLEY, G.M. & KERSHAW, A.P., 1994. Late Quaternary environmental change and human impact around Lake Bolac, western Victoria, Australia. *Journal of Quaternary Sciences*, 9: 367-377.

D'COSTA, D.M., 1997. *The Reconstruction of Quaternary Vegetation and Climate on King Island, Bass Strait, Australia*. Unpublished PhD thesis, Department of Geography and Environmental Science, Monash University, Clayton.

D'COSTA, D.M. & KERSHAW, A.P., 1995. A Late Pleistocene and Holocene pollen record from Lake Terang, Western Plains of Victoria, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 113: 57-67.

D'COSTA, D. & KERSHAW, A.P. 1997. An expanded recent pollen database from South-eastern Australia and its potential for refinement of palaeoclimatic estimates. *Australian Journal of Botany*, 45: 583-605.

D'COSTA, D.M., EDNEY, P., KERSHAW, A.P. & DE DECKKER, P., 1989. Late Quaternary palaeoecology of Tower Hill, Victoria, Australia. *Journal of Biogeography*, 16: 461-482.

DETTMAN, M.E., POCKNALL, D.T., ROMERO, E.J. AND DEL CARMEN ZAMALOA, M.,1990. Nothofagadites *Erdtman ex Potoni, 1960; a catalogue of species with notes on the paleogeographic distribution of* Nothofagus *Bl. (Southern Beech)*. New Zealand Geological Survey Paleontogical Bulletin 60, 79 pp.

DODSON, J.R., 1974a. Vegetation and climatic history near Lake Keilambete, western Victoria. *Australian Journal of Botany*, 22: 709-17.

DODSON, J.R., 1974b. Vegetation history and water fluctuations at Lake Leake, southeastern South Australia I. 10,000 BP to present. *Australian Journal of Botany*, 22: 710-741.

DODSON, J.R., 1975. Vegetation history and water fluctuations at Lake Leake, south-eastern South Australia. II 50,000 BP to 10,000 BP. *Australian Journal of Botany*, 23: 815-31.

DODSON, J.R., 1977. Pollen deposition in a small enclosed drainage basin lake. *Review Palaeobotany and Palynology*, 24: 179-193.

DODSON, J.R. 1979. Late Pleistocene vegetation and environments near Lake Bullenmerri, Western Victoria. *Australian Journal of Ecology*, 4: 419-427.

DODSON, J.R., 1982/1983. Modern pollen rain in southeastern New South Wales, Australia. *Review of Palaeobotany and Palynology*, 38: 249-268.

EDNEY, P.A., 1987. *Late Quaternary vegetation and environments from Lake Wangoom, western*

Victoria. Unpublished MA thesis, Monash University, Melbourne.

EDNEY, P.A., KERSHAW, A.P. & DE DECKKER, P., 1990. A Late Pleistocene and Holocene vegetation and environmental record from Lake Wangoom, Western Plains of Victoria. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 80: 325-343.

FAEGRI, K. & IVERSEN, J. 1989. *Textbook of Pollen Analysis.* 4th Edition with K. Kryzwinski. John Wiley: Chichester and New York.

FEUER, S. & TOMB, A.S., 1977. Pollen morphology and detailed structure of Family Compositae, Tribe Cichorieae. II Subtribe Microseridinae. *American Journal of Botany,* 64(2): 230-245.

FLOOD, J., 1995. *Archaeology of the Dreamtime.* Angus and Robertson, Sydney, Australia, 328 pp.

GELL, P.A., BARKER, P.A., DeDECKKER, P., LAST, W.M. & JELICIC, L., 1994. The Holocene history of West Basin Lake, Victoria, Australia; chemical changes based on fossil biota and sediment mineralogy. *Journal of Paleolimnology,* 12: 235-258.

GRIMM, E. C., 1991. *Tilia version 1.12 and Tiliagraph.* Illinois State Museum, Springfield, U.S.A.

HARLE, K.J., 1998. *Patterns of vegetation and climate change in southwest Victoria over approximately the last 200,000 years.* Unpublished PhD thesis, Monash University, Melbourne.

HARLE, K.J., KERSHAW, A.P. & HEIJNIS, H., 1999. The contributions of uranium/thorium and marine palynology to the dating of the Lake Wangoom pollen record, western plains of Victoria, Australia. *Quaternary International,* 57/58: 25-34.

HARLE, K.J., HEIJNIS, H., CHISARI, R., KERSHAW, A.P., ZOPPI, U. & JACOBSEN, G., 2002. A chronology for the long pollen record from Lake Wangoom, western Victoria (Australia) as derived from uranium/thorium disequilibrium dating. *Journal of Quaternary Science,* 17 (7): 707-720.

HARRIS, W.F. & NORRIS, G., 1972. Ecologic significance of recurrent groups of pollen and spores in Quaternary sequences from New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 11: 107-124.

HEAD, L.M., 1984. *Environment as Artefact: A Palaeoecological contribution to the Prehistory of Southwestern Victoria.* PhD Thesis, Monash University.

HEAD, L., 1988. Holocene vegetation, fire and environmental history of the Discovery Bay region, southwestern Victoria. *Australian Journal of Ecology,* 13: 21-49.

HEKEL, H., 1972. *Pollen and spore assemblages from Queensland Tertiary sediments.* Geological Survey of Queensland, Publication 355, 34pp.

HESSE, P., 1994. The record of continental dust from Australia in Tasman Sea sediments. *Quaternary Science Reviews,* 13: 257-272.

HILL, R.S. & MACPHAIL, M.K., 1985. A fossil flora from Tasmania. *Australian Journal of Botany,* 33: 497-517.

HNATIUK, R.J., 1990. *Census of Australian Vascular Plants. Australian Flora and Fauna Series no. 11,* Bureau of Flora and Fauna, Canberra, Australian Government Publishing Services, Canberra, 650 pp.

HOPE, G.S., 1974. The vegetation history from 6000 B.P. to Present of Wilson's Promontory, Victoria, Australia. *New Phytology,* 73: 1035-1053.

JONES, R., 1969. Fire-stick farming. *Australian Natural History,* 16: 224-228.

JONES, R., 1975. The Neolithic Palaeolithic and hunting gardeners: man and land in the Antipodes. In *Quaternary Studies,* R.P. Suggate & M.M. Cresswell eds, Royal Society of New Zealand, Wellington, 21-34.

KERSHAW, A.P., 1970. Pollen morphological variation within the Casuarinaceae. *Pollen et Spores* XII, 3: 491-507.

KERSHAW, A.P., 1976. A late Pleistocene and Holocene pollen diagram from Lynch's Crater, northeastern Queensland, Australia. *New Phytologist,* 77: 469-498.

KERSHAW, A.P., 1985. An extended late Quaternary vegetation record from north-eastern Queensland and its implications for the seasonal tropics of Australia. *Proceedings of the Ecological Society of Australia,* 13: 179-189.

KERSHAW, A.P., 1986. The last two glacial-interglacial cycles from northeastern Australia: implications for climatic change and Aboriginal burning. *Nature,* 322: 47-49.

KERSHAW, A.P., 1988. Australasia. In *Vegetation History,* B. Huntley & T. Webb III, eds, Kluwer, Academic Publishers, 238-306.

KERSHAW, A.P., 1993. Palynology, biostratigraphy and human impact. *The Artefact,* 16: 12-18.

KERSHAW, A.P., CLARK, J.S., GILL, A.M. & D'COSTA,

D.M., 2002. *A history of fire in Australia. In Flammable Australia: the fire regimes and biodiversity of a continent*, R. Bradstock, J. Williams & A.M. Gill, eds, Cambridge University Press, 3-25.

KERSHAW, A.P., BULMAN, D. & BUSBY, J., 1994a. An examination of modern and pre-European settlement pollen samples from southeastern Australia-assessment of their application to quantitative reconstruction of past vegetation and climate. *Review of Palaeobotany and Palynology,* 82: 83-96.

KERSHAW, A.P., D'COSTA, A.M., TIBBY, J., WAGSTAFF, B.E. & HEIJNIS, H., 2004. The last million years around Lake Keilambete, western Victoria. Proceedings of the Royal Society of Victoria 116(1): 95-106.

KERSHAW, A.P., MARTIN, H.A. & MCEWEN MASON, J.R.C., 1994. The Neogene: a period of transition. In *History of the Australian vegetation: Cretaceous to Recent*, R.S. Hill, ed., Cambridge University Press, Cambridge, 299-327.

KERSHAW, A.P., MCKENZIE, G.M. & MCMINN, A., 1993. A Quaternary vegetation history of northeastern Queensland from pollen analysis of ODP site 820. *Proceedings of the Ocean Drilling Program, Scientific Results,* 13: 107-114.

KRON, K.A., JUDD, W.S., STEVENS, P.F, CRAYN, D.M., ANDERBERG, A.A, GADEK, P.A, QUINN, C.J. & LUTEYN, J.L., 2002. Phylogenetic Classification of Ericaceae: Molecular and Morphological Evidence. *The Botanical Review,* 68(3): 335-423.

LONGMORE, M.E., 1997. Quaternary palynological records from perched lake sediments, Fraser Island, Queensland, Australia: rainforest, forest history and climatic control. *Australian Journal of Botany,* 45: 507-526.

LONGMORE, M.E. & HEIJNIS, H., 1999. Aridity in Australia: Pleistocene records of palaeoecological change from the perched lake sediments of Fraser Island, Queensland, Australia. *Quaternary International, Quaternary International,* 57/58: 35-48.

LULY, J.G., 1993. Holocene palaeoenvironments near Lake Tyrell, semi-arid northwestern Victoria, Australia. *Journal of Biogeography,* 20: 587-598.

MACPHAIL, M.K., 1979. Vegetation and climates in southern Tasmania since the last glaciation. *Quaternary Research,* 11: 306-41.

MARTIN, H.A., 1989. Evolution of Mallee and its environment. In *Mediterranean Landscapes in Australia,* J.C. Noble & R.A. Bradstock, eds, CSIRO, Melbourne, 83-92.

MARTIN, H.A., 1990. The palynology of the Namba Formation in Wooltana-1 bore, Callabona Basin (Lake Frome), South Australia and its relevance to Miocene grasslands in Central Australia. *Alcheringa,* 14: 247-55.

MARTINSON, D.G., PISIAS, N.G., HAYS, J.D., IMBRIE, J., MOORE JR, T.C. & SHACKLETON, M.J., 1987. Age dating and the Orbital Theory of the Ice Ages: development of a high-resolution 0 to 300,000-year chronostratigraphy. *Quaternary Research,* 27: 1-29.

MCEWAN-MASON, J.R.C., 1991. The late Cainozoic magnetostratigraphy and preliminary palynology of Lake George, New South Wales. In *The Cainozoic in Australia: A Reappraisal of the Evidence,* M.A.J. Williams, P. De Deckker & A.P. Kershaw, eds, Geological Society of Australia, Melbourne, 195-209.

MCKENZIE, G.M., 1989. *Late Quaternary vegetation and climate in the Central Highlands of Victoria, with special reference to* Nothofagus cunninghamii *(Hook.) Oerst. rainforest.* Unpublished PhD thesis, Monash University, Victoria, Australia.

MOSS, P.T. & KERSHAW, A.P., 2000. The last glacial cycle from the humid tropics of northeastern Australia: comparison of a terrestrial and a marine record. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 155: 155-176.

NICHOLSON, P.H., 1993. Fire and the Australian Aborigine - an enigma. In *Fire and the Australian Biota,* second edition, A.M. Gill, R.H. Groves & I.R. Noble, eds, Australian Academy of Science, Canberra, 55-76.

OLLIER, C.D., 1967. Landforms of the Newer Volcanic Province of Victoria. In *Landform Studies from Australia and New Guinea,* J.N. Jennings & J.A. Mabbutt, eds, Australian University Press, Canberra, 315-319.

OVERPECK, J.T., PRENTICE, I.C. & WEBB III, T., 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research:* 23, 87-108.

PARKINSON, G. (ed.), 1986. *Atlas of Australian Resources. Volume 4: Climate.* Australian Surveying and Land Information Group, Austral-

ian Government Publishing Service, Canberra.

PRENTICE, I.C., 1980. Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. *Review of Palaeobotany and Palynology*, 31: 71-104

ROBINSON, L., 1997. *Field Guide to the native Plants of Sydney*. (2nd Edition). Kangaroo Press. 448 pp.

SAYERS, C.E., 1972. *Of Many Things*. Olinda Books, Victoria.

SCARLETT, N.H., WALLBRINK, S.J. & McDOUGALL, K., 1993. *Field Guide to Victoria's Native Grasslands*. Victoria Press, South Melbourne. 190pp.

SHERWOOD, J., OYSTON, B. & KERSHAW, A.P., 2004. The Age of Tower Hill Volcano, southwest Victoria, Australia. *Proceedings of the Royal Society of Victoria*, 116(1): This volume.

SINGH, G. & GEISSLER, E.A., 1985. Late Cainozoic history of vegetation, fire, lake levels, and climate at Lake George, New South Wales. *Philosophical Transactions of the Royal Society of London, Series B*, 311: 379-477.

SINGH, G., KERSHAW, A.P. & CLARK, R., 1993. Quaternary vegetation and fire history in Australia. In *Fire and the Australian Biota*, second edition, A.M. Gill, R.H. Groves & I.R. Noble, eds, Australian Academy of Science, Canberra, 23-54.

SPECHT, R.L., 1981a. Major vegetation formations in Australia. In *Ecological Biogeography of Australia*, A. Keast, ed., Dr W. Junk bv Publishers, The Hague, 163-297.

SPECHT, R.L., 1981b. Ecophysiological principles determining the biogeography of major vegetation formations in Australia. In *Ecological Biogeography of Australia*, A. Keast, ed., Dr W. Junk bv Publishers, The Hague, 299-333.

SPECHT, R.L., 1994. Heathlands. In *Australian Vegetation*, R.H. Groves, ed., Cambridge University Press, Cambridge, 321-344.

STOVER, L.E. & PARTRIDGE, A.D., 1973. Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, southeastern Australia. *Proceedings of the Royal Society of Victoria*, 85: 237-286.

TINDALE, A.B., 1959. Ecology of primitive Aboriginal man in Australia. *Monographiae Biologicae*, 8: 36-51.

WAGSTAFF, B.E., KERSHAW, A.P., O'SULLIVAN, P.B., HARLE, K.J. & EDWARDS, J., 2001. An Early to Middle Pleistocene palynological record from the volcanic crater of Pejark Marsh, Western Plains of Victoria, southeastern Australia. *Quaternary International* 83-85: 211-232.

WALSH, N.G. & ENTWISLE, T.J. (eds), 1996. *Flora of Victoria*. Inkata Press, Melbourne.

WINKLER, M.G., 1985. Charcoal analysis for paleoenvironmental interpretation: a chemical assay. *Quaternary Research* 23: 313-326.

WODEHOUSE, R.P., 1935. *Pollen Grains*. McGraw-Hill, New York.